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STUDIES OF COMBINING ABILITY IN BROMEGRASS AND CRESTED WHEATGRASS[1]

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The recognition of combining ability as an important factor in the selection of plants and inbred lines in corn has stimulated considerable interest in the possibilities of selecting other cross-pollinated crops upon a similar basis. Studies of combining ability have been quite extensive in alfalfa and breeders of this crop have suggested methods by which plants with good combining ability may be used to produce high yielding synthetic varieties and commercial hybrids. Selection in perennial forage grasses on the basis of combining ability is being practised at plant breeding stations in North America at the present time but as yet there is little published evidence of the success of selection on this basis or of the breeding techniques by which combining ability may be evaluated.

Investigations were undertaken at Saskatoon in bromegrass and crested wheatgrass to assess the range of interplant variation in combining ability and to compare the reliability of various kinds of progenies which might be used in determining the combining ability of individual plants. Data were analysed to show the relationship of specific combining ability, or the response of plants in particular crosses, to general combining ability, or the average response of plants in crosses. Correlations of the performances of parent plants and progeny classes also were made to provide indications of the heritability of yield and other characters.

LITERATURE REVIEW

The use of inbred lines in breeding bromegrass was reported by Kirk (14, 15), Popravko (22), Stevenson (26), Hayes and Schmid (9), and Tsiang (29). The species was found to be largely self-sterile yet containing partially self-fertile plants in sufficient numbers to permit the production of selfed lines. Selfing caused reductions in vigour and fertility of lines and consequent difficulties in carrying them to advanced generations of inbreeding. Hayes and Schmid (9) produced a limited number of single crosses which outyielded the commercial variety.

Hill and Myers (10) reviewed the literature on chromosome numbers in bromegrass and reported an extensive study of strains of various origins. They found a chromosome number of 56 (2n) for 192 of 193 plants studied. The single variant had 8 to 11 accessory chromosome fragments in addition to the regular complement. Elliott and Love (5) found marked irregularity

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in the meiotic behaviour of bromegrass and suggested that non-random selection of gametes might be anticipated. Elliott and Wilsie (6) observed good fertility and regularly normal bivalent association at meiosis in a haploid plant. This they regarded as evidence of an autopolyploid derivation for the species.

The nomenclature recommended by Dillman (4) has been accepted by the present writer in discussing the Fairway and Standard types of crested wheatgrass. The shorter growing, finer stemmed, and more leafy Fairway type was classified by Dillman as *Agropyron cristatum* (L.) Gaertn., and the taller growing, coarser Standard type as *A. desertorum* (Fisch.) Schult. Dillman found the Fairway and Standard types to have 2n chromosome numbers of 14 to 28, respectively. This is in agreement with the results of Peto (21), Myers and Hill (19), and Murphy (18) but these authors also observed aneuploid plants with from one to three chromosomes in addition to the normal number in the Standard type. Myers and Hill considered the Standard type to be an autopolyploid in view of the high degree of quadrivalent association of chromosomes at meiosis. Murphy (18), and Cheng (2) indicated that both types were sufficiently self-sterile to prevent selfed line methods of breeding. Stevenson (27) indicated the unsuitability of inbreeding techniques in crested wheatgrass as inbred lines showed marked loss of vigour.

Extensive studies of combining ability, or the ability of plants or lines to transmit desirable qualities to their crosses, were undertaken in corn coincident with the development of hybrid programmes. Jenkins and Brunson (11) found that combining ability as indicated by single crosses was closely correlated with combining ability as shown in inbred-variety crosses. To expedite the testing of lines Sprague (24) advocated testing in early generations even to the extent of testing original non-inbred (So) plants. Evidence of the heritability of combining ability in corn has been given by Sprague (24), Johnson and Hayes (12), Cowan (3), and Green (8). Sprague and Tatum (25) described "general combining ability" as the average performance of lines in hybrid combinations and distinguished it from "specific combining ability" or the ability of lines to perform relatively better or more poorly in crosses than would be expected on the basis of average performance. Green (7) and Keller (13) showed that specificity of combining ability was exhibited by other than inbred material. When single F_2 plants were tested in top-crosses to tester hybrids and varieties there was significant variation in the order of F_2 plants for combining ability depending on the tester used. Robinson *et al.* (23) studied character heritability in corn crosses by analysis of variance methods and progeny-parent regressions. Heritabilities for various morphological characters such as plant height and ear height were notably higher than that for yield.

Tysdal and associates in Nebraska (30, 31, 32) and Bolton and Stevenson in Canada (1, 28) applied combining ability concept to the breeding of alfalfa. In particular, they developed breeding techniques by which plants with high combining ability suitable for inclusion in strain building plots may be identified. While single crosses were used for critical tests of the combining ability of single plants Tysdal *et al.* (30) also proposed polycross nurseries to obtain seed of a large number of selected plants

simultaneously. In this method plants or lines to be tested were placed together in isolated nurseries and allowed to interpollinate. Replication and randomization of plants or lines in the polycross were suggested to insure random pollination and to provide a bulk of seed sufficient for regional tests.

Tysdal and Crandall (32) compared the combining ability rating of seven plants of alfalfa as shown by polycross yields with the rating as indicated by the average yields of three to five single crosses. Good correspondence was found. They also obtained good agreement between polycross progeny yields and top-cross yields where the top-cross was made between each clone and a commercial variety. Fair agreement only was indicated for the comparison of polycross progeny yields and the yields of modified top-crosses produced by growing the commercial variety in alternate rows between rows of the selections. Bolton (1) investigated the use of single clones as testers for other selected plants. The yields of tester-crosses when compared with the average yields of single crosses gave correlation coefficients of + 0.657 and + 0.671 for yields of seed and +0.644 and + 0.939 for yields of forage. The use of high yielding plants as testers gave similar results to those from using low yielding plants. Increasing the number of tester plants from one to two or to four did not materially increase the efficiency of the test for combining ability.

The results of Tysdal and Crandall (32) indicated that marked breeding progress could be achieved by the selection of alfalfa plants with high combining ability. Eight synthetics were found to give yields in accordance with those predicted from combining ability tests of plants constituting them. The highest yielding synthetic yielded 116 per cent of the commercial variety and the average polycross progeny yields of parent plants entering the synthetic was 111 per cent of the commercial variety.

MATERIALS AND METHODS

Studies of combining ability were conducted in bromegrass, *Bromus inermis* Leyss., crested wheatgrass of the Fairway type, *Agropyron cristatum* (L.) Gaertn., and crested wheatgrass of the Standard type, *A. desertorum* (Fisch.) Schult. In each species the method of study was to intercross a small number of selected plants in all single cross combinations and relate the performance of resultant progenies with that of progenies derived from open-pollination and polycrosses and with the parental clones. Yield of forage was the main consideration throughout all comparisons but since bromegrass is a rhizomatous species observations also were made in this grass of the degree of creeping. In the Standard type of crested wheatgrass an infestation of the western wheat aphis (*Brachycolus tritici* Gill.) in progeny nurseries allowed the observation of strain resistance to this pest.

Plant Materials

Single crosses in bromegrass were made among seven plants of the Superior variety. This strain is similar to the northern commercial type of bromegrass, differing from it mainly in being less strongly creeping. Plants used in this study had no other previous breeding history and were selected in space-planted nurseries as having superior height, leafiness, and

resistance to leaf-spot diseases. Selection also was based upon high self-sterility but, as will be shown later, plants were less self-sterile than preliminary tests had indicated. The plants were selected from an original population of 266 thus giving a selection intensity of 2.6 per cent.

Single crosses in the Fairway type of crested wheatgrass were made within one group of nine plants which had no previous breeding history and a second group of seven plants which had been inbred. Inbred plants consisted of two plants from each of inbred lines A, C, and D, and one from inbred line B. These lines had been inbred for one generation except for line A which had been inbred for three generations. Crosses in the Standard type of crested wheatgrass were made among seven plants of a commercial lot. All plants of crested wheatgrass were selected from single plant nurseries as having good height, leafiness and vigour, and also a high degree of self-sterility as shown in preliminary tests. The intensity of selection for the non-inbred group of Fairway material was 7 per cent and for both the Fairway and the Standard type plants the intensity of selection was 10 per cent.

The methods of producing crossed seed for these studies were similar to those described by Knowles and Horner (16) for crested wheatgrass. These consisted essentially of the bulk transference of pollen between highly self-sterile plants without any emasculation. Bromegrass crosses were made mainly by the method of bag-switching, that is, an exchange of pollination bags between pairs of plants when flowering was in progress. Crested wheatgrass crosses were made by bag-switching and by the mutual pollination of clones planted together in paired combinations. Open-pollination progenies were grown from seed obtained from the original selections following natural pollination in the field. In bromegrass such seed was harvested from clonal rows of a reserve nursery containing a total of 120 clonal lines. This nursery contained two replications with clones randomized in each replication. Progenies grown from seed of clones in the first replication of this nursery will be referred to as "Open-pollination progenies Source-1", and from the second replication as "Open-pollination progenies Source-2". Open-pollination seed of crested wheatgrass was collected from the original selected plants growing in observation nurseries at a spacing of 3 ft. $\times$ 3 ft.

Polycross seed of bromegrass was obtained from an isolated plot in which the seven selected plants and three additional plants were each represented by four separate clones. Clones were arranged in the polycross plot in four replicates with a clone of each of the ten strains being placed at random in each replicate block. Polycross seed was not obtained for crested wheatgrass but top-crossed seed was available for five of the nine plants of the Fairway group. Pollinations in this case were made with the pollen gun using bulk pollen collected from 20 random plants of the Fairway variety.

Establishment of Field Trials

All material was tested under space-planted conditions in the field. Seedlings and clones were started in the greenhouse and transplanted to the field in June 1947. Clonal establishment was less successful than

seedling establishment particularly in crested wheat grass. Each of the four groups of controlled crosses and related progenies was grown in a separate yield test. Triple lattice repeated designs with six replications were used in all trials. The tests of bromegrass and of non-inbred Fairway crested wheatgrass each included a total of 64 strains while the tests of inbred Fairway and Standard crested wheatgrass contained 49 entries. Plots consisted of single rows 16 to 20 feet in length with rows spaced three feet apart from bromegrass and two feet apart for crested wheatgrass. Plant spacing within the rows was two feet except in the test of the Standard type of crested wheatgrass where a spacing of one and one-half feet was used. In each trial all possible single crosses between parent plants were represented and in three of the four groups of plants several reciprocal single crosses were present.

Check strains in the test of bromegrass included the Superior variety, northern commercial bromegrass purchased from a local seed house, the Achenbach variety obtained from Kansas State College, Manhattan, Kansas and the Parkland variety maintained at the Dominion Forage Crops Laboratory, Saskatoon. Checks in tests of the Fairway type of crested wheatgrass consisted of the Fairway variety and strains S-39-$\overline{3}$-1, S-38-$\overline{9}$-$\overline{1}$-3, S-39-$\overline{7}$-1, and S-32-$\overline{28}$-1-1 each developed by the isolated increase of lines originally derived from inbreeding. Check lots in the test of the Standard type of crested wheatgrass were S-1333, S-131, Standard and Forage. Strains S-1333 and S-131 represent preliminary strains of the Standard type developed by the increase of introductions from the United States Department of Agriculture and the U.S.S.R., respectively. The Standard strain was obtained from the United States Department of Agriculture and traced to the introduction S.P.I. 19537. The Forage strain was developed at the Dominion Forage Crops Laboratory by the increase of a single plant selection. This strain was rather extensively distributed in Saskatchewan in 1935 and 1936 but never licensed as a variety. It is probable that much of the commercial seed of the Standard type produced in Saskatchewan to-day traces to this source.

Nature of Observations

Yields of hay in terms of green weight, and other observational data were obtained in 1948. The percentages of original plants that were missing at harvest-time were also noted and found to be respectively 6.0, 2.6, 10.0 and 3.5 for tests of bromegrass, non-inbred Fairway crested wheatgrass, inbred Fairway crested wheatgrass, and Standard crested wheatgrass. Yields per plot were corrected for the number of missing plants by direct linear corrections. For example, the harvested yields of 11-plant plots were multiplied by the factor 11/10 when one plant was missing. In bromegrass the degree of creeping was determined by measuring the diameter of spread of three plants in each plot. These measurements were made immediately after plots were cut for hay in the second year of growth. In view of the minor degree of leaf spot infection in bromegrass in 1948 it was not possible to compare strains in regard to disease resistance. In 1948 all parent plants involved in these studies were retested for self-sterility by placing 12 selfing bags on clones of each plant.

TABLE 1.—AVERAGE YIELDS IN POUNDS GREEN WEIGHT PER PLOT OF SINGLE CROSSES AMONG SEVEN SELECTED PLANTS OF BROMEGRASS COMPARED TO THE YIELDS OF OPEN-POLLINATION PROGENIES, POLYCROSS PROGENIES, PARENT CLONES, AND CHECK VARIETIES (SIX-REPLICATE TEST OF 64 ENTRIES, PLANTED, JUNE 1947, HARVESTED, JULY 1948, YIELDS CORRECTED BY COVARIANCE FOR DEGREE OF CREEPING)

Selection	Single cross when selection in column one crossed with:						Average of single crosses	Open-pollination progeny		Polycross progeny	Parent clone
	18	19	83	85	87	90		Source-1	Source-2		
16	— 11.5	11.6 —	12.2* 12.4	11.2 9.1	9.5 10.8	13.1 12.6	11.8	12.2	13.0	12.6	9.5
18		— 12.5	10.0 11.2	11.7 9.1	12.4 —	11.3 12.9	12.0	11.6	12.3	12.8	11.1
19			12.4 12.0	12.1 —	— 10.0	12.1 —	11.8	12.5	11.8	12.4	9.4
83				10.2 9.4	11.7 12.0	9.0 —	11.2	11.9	11.4	12.9	10.9
85					9.4 —	9.8 14.3	11.5	12.9	—	12.6	9.2
87						11.8 —	11.1	12.1	12.2	13.0	11.7
90							12.2	13.8	13.8	12.9	13.3
Range							1.1	2.2	—	0.6	4.1
Average							11.7	12.4	—	12.7	10.7
Average all crosses and progenies							11.8				
Checks—Superior							12.7				
Commercial (1)							12.5				
Commercial (2)							12.8				
Parkland							10.2				
Achenbach							13.1				
Av. checks							12.3				

	Difference in creeping of mean		
	0 in.	4 in.	8 in.
L.S.D. (P = 0.05)—means of 6 plots	1.5	1.5	1.6
means of 36 plots	0.6	0.6	0.7
means of 6 and 36 plots	1.2	—	—

* The upper value in each cell indicates the yield of the cross when the selection in column one was used as the female parent, i.e. 16 × 83. The lower value in each cell indicates the yield of the reciprocal cross, or 83 × 16.

Differential damage to strains of the Standard type of crested wheatgrass from infestations of the western wheat aphis (*Brachycolus tritici* Gill.) was noted in the spring of 1948. Damage consisted of a marked dwarfing of plants similar to that caused by this same pest in winter wheat (20). Negligible effects were noted in the Fairway type of crested wheatgrass and no damage of any kind in bromegrass. Plots within the test of intercrosses of the Standard type were scored from 1 to 10 for resistance to damage with a score of 1 representing very severe effects and a score of 10 no injury.

EXPERIMENTAL RESULTS

Bromegrass

Analyses of variance for the test of bromegrass material indicated highly significant differences among the 64 strains entering the test both for yield of forage and for degree of creeping. The coefficients of variability in these analyses were 12 per cent with respect to yield and 17 per cent with regard to the degree of creeping. Analyses of variance as for a lattice design resulted in a gain in efficiency of 11 per cent in testing for yield and no gain in efficiency in testing for degree of creeping. A significant relationship ($r = +0.63$) was found between yield and the degree of creeping and yields were corrected for the degree of creeping by covariance methods. Since small gains in efficiency were obtained by using lattice methods of analysis, the method of analysis as for a randomized block design was used throughout for variance and covariance determinations.

Hay yield data are presented in Table 1 and the degree of creeping data in Table 2. Least significant differences based on means of 6 plots are given for the comparison of individual strains, and on means of 36 plots for the comparison of the average response of single crosses for different selections. Least significant yield differences also are noted where strains differ in degree of creeping. Least significant differences based on means of 6 and 36 plots are included for the comparison of individual strains and averages of single crosses. A subdivision of strain variance according to types of progenies and clones in the test has been provided in Table 3.

Data in Table 1 indicate considerable variation in the yields of reciprocal crosses. Poor correspondence of reciprocals apparently resulted from partial self-fertility of certain selections and the inclusion of selfed plants within some of the single crosses. In tests of self-fertility in 1948 it was found that selections 85 and 83 produced 22.1 and 12.8 seeds per panicle, respectively when selfed whereas other selections when self-pollinated gave fewer than three seeds per panicle. In progenies of crosses between plants 16 and 85, 18 and 85, and 90 and 85 there were significant differences between the yields of reciprocal crosses with the low yielding reciprocal in each case arising from the use of plant 85 as the female parent. The cross between plants 90 and 18 also showed a significant difference in the yield of reciprocals but in this instance both parents were moderately self-sterile in selfing tests. However, a high percentage of small plants in the cross 18×85 indicated that here again the difference between the yield of reciprocal crosses was due to the contamination of crosses by plants derived from selfing. To reduce the effect of selfing in determining the average yield of single crosses only the member of the reciprocal pair show-

TABLE 2.—THE AVERAGE DEGREE OF CREEPING IN INCHES OF SINGLE CROSSES AMONG SEVEN SELECTED PLANTS OF BROMEGRASS COMPARED TO THOSE OF OPEN-POLLINATION PROGENIES, POLYCROSS PROGENIES, PARENT CLONES AND CHECK VARIETIES (SIX-REPLICATE TEST OF 64 ENTRIES, PLANTED, JUNE 1947, DEGREE OF CREEPING MEASURED, JULY 1948)

Selection	Single cross when selection in column one crossed with:						Average of single crosses	Open-pollination progeny		Polycross progeny	Parent clone
	18	19	83	85	87	90		Source-1	Source-2		
16	17.5	18.0 —	17.5* 17.7	22.2 16.5	15.2 14.5	23.5 21.3	18.9	18.0	19.8	19.7	19.3
18		— 15.0	12.0 11.8	14.3 15.8	15.0 —	15.5 19.0	15.4	15.8	14.0	15.8	12.0
19			15.5 16.7	16.5 —	— 17.2	17.7 —	16.6	13.5	15.7	17.5	15.2
83				13.7 16.3	13.2 13.7	15.0 —	14.6	12.2	13.2	17.0	12.0
85					17.0	18.5 22.5	17.7	17.0	—	15.8	18.5
87						17.3 —	15.8	13.2	16.5	16.2	12.0
90							19.2	19.3	23.7	21.8	21.2
Range							4.6	7.1	—	6.0	9.2
Average							16.9	15.6	—	17.7	15.7
Average all crosses and progenies							16.7				
Checks—Superior							15.2				
Commercial (1)							19.3				
Commercial (2)							19.7				
Parkland							11.2				
Achenbach							19.5				
Av. checks							17.0				

L.S.D. (P = 0.05)—means of 6 plots 3.3
means of 36 plots 1.3
means of 6 and 36 plots 2.5

* The upper value in each cell indicates the degree of creeping of the cross when the selection in column one was the female parent of the cross, i.e. 16 × 83. The lower value in each cell represents the reciprocal cross, or 83 × 16.

ing the higher yield was used for averaging purposes. The member of the reciprocal pair used in calculating average yields was again used in determining the average degree of creeping for single crosses. Only one cross of the group was outstanding for yield. This cross, 90 × 85, showed a yield of 14.3 pounds per plot which is significantly above the yield of 12.7 for the Superior variety from which selections were made.

Table 3 indicates the significance of yield and creeping differences noted in Tables 1 and 2. There were significant differences in yield and degree of creeping among clones, among single crosses, and among open-pollination progenies. For polycross progenies no significance was shown between progenies for yield although there was for the creeping habit. Clones of selections were significantly lower yielding and less strongly creeping than progenies. Single crosses were on the average significantly lower yielding than the other types of progenies. Polycrosses and open-pollination progenies gave similar yields on the average although polycrosses were on the average more strongly creeping than open-pollination progenies. It is interesting to note the absence of a significant interaction between the yield of open-pollination progenies and the source of the seed giving rise to these progenies. On the other hand the significant interaction for the creeping habit indicates that open-pollination progenies derived from Source-1 did not correspond completely with those from Source-2.

The greatest range in yield as indicated in Table 1 occurred within single crosses. The difference between the highest and lowest yielding crosses was 5.3 pounds per plot. The range for the average yield of single crosses was only 1.1 pounds per plot but significance was still shown. Progenies from open-pollination gave a range of 2.2 pounds per plot with differences between strains being significant. For polycross progenies

TABLE 3.—SUBDIVISION OF DEGREES OF FREEDOM AND STRAIN VARIANCE FOR 64 PROGENIES AND CLONES OF BROMEGRASS (YIELDS CORRECTED BY COVARIANCE FOR DEGREE OF CREEPING)

Factor	Degrees of freedom	Mean square	
		Yield	Creeping habit
Checks vs. others	1	11.00*	4.34
Within checks	4	7.21**	84.28**
Clones vs. progenies	1	34.76**	33.03*
Within clones	6	13.57**	92.27**
Single crosses vs. polycrosses and open-pollination progenies	1	112.61**	0.35
Within single crosses	31	10.62**	47.85**
Polycrosses vs. open-pollination progenies	1	3.12	57.30**
Within polycrosses	6	0.24	31.44**
Open-pollination progeny of selection 85 vs. remaining open-pollination progenies	1	1.74	3.98
Between remaining open-pollination progenies	5	5.74**	133.45**
Source of open-pollination progenies	1	0.0	7.00
Source × strain of open-pollination progenies	5	1.40	22.38*
Error—Yield	314	1.71	—
—Creeping habit	315	—	7.96

* Significance P = 0.05.
** Significance P = 0.01.

there was a range of only 0.6 pounds per plot with the differences between selections not exceeding the least significant difference. The range in yield of parent clones of 4.1 pounds per plot was exceeded only by the range for individual crosses. The range in degree of creeping was greatest for individual single crosses (11.7 inches), followed by parent clones (9.2 inches), open-pollination progenies (7.1 inches), polycross progenies (6.0 inches), and the average of single crosses (4.6 inches). The decrease in range of variation of creeping in polycrosses was similar to that shown for yield.

The extent to which the different progeny classes indicated similar combining ability was obtained by making simple correlations between the yields of various progeny classes for each selection. Table 4 presents correlation coefficients obtained from the comparisons of such progeny classes with one another and also comparisons of progeny classes with parent clones. There were no significant correlations between the yields of the different types of progenies although a strong positive relationship was suggested between the yields of open-pollination progenies from the two nursery sources and also between the average yield of single crosses and open-pollination progenies Source-2. Correlations between polycross progenies and single crosses and between polycross progenies and open-pollination progenies were very low. The poor relationship of polycross progeny yields to the yields of other progeny types and the low range of yield among polycross progenies are factors which indicate that the latter may be less suitable than open-pollination progenies for tests of combining ability. Definite conclusions in this regard cannot be made in view of the lack of precision in testing procedure and the limited number of original plants involved in these studies. Much higher correlations were obtained for the creeping habit than for yield. Significant correlations were shown between most of the progeny classes and parent clones. Correlations involving polycross progenies were somewhat lower than correlations involving other progeny classes. It is difficult to determine which progeny class gave the most reliable index of parent character but considering the fairly high relationship between different progenies the degree of creeping shown by any one type may be taken as indicative of breeding characteristics of the parents.

Comparisons of parental clonal lines and their respective progeny classes (Table 4) give indications of the degree to which yield and the degree of creeping were inherited. Correlation coefficients of $+0.21$, $+0.35$, and $+0.80$ were obtained in the comparison of parent yields and the yields of single crosses, open-pollination progenies, and polycross progenies, respectively. Comparisons of the degree of creeping of parent clones and progenies gave correlation coefficients of $+0.97$, $+0.87$, and $+0.74$ for single crosses, open-pollination progenies, and polycross progenies, respectively. It would appear that the spreading character is highly heritable and that rapid changes in the degree of creeping can be accomplished on the basis of selection in parent clonal lines. For yield, however, with a parental range and precision of testing such as encountered in these trials, it would seem that little correspondence may be expected between parent and progeny performance.

TABLE 4.—CORRELATION COEFFICIENTS FOR FORAGE YIELDS AND FOR DEGREES OF CREEPING AS SHOWN BY SINGLE CROSSES, OPEN-POLLINATION PROGENIES, POLYCROSS PROGENIES, AND PARENT CLONES OF SEVEN SELECTED PLANTS OF BROMEGRASS

Comparison	n	r	
		Yield	Creep
Single cross averages and open-pollination progenies Source-1	7	+ 0.44	+ 0.88**
Single cross averages and open-pollination progenies Source-2	6	+ 0.68	+ 0.94**
Single cross averages and polycross progenies	7	− 0.30	+ 0.75*
Open-pollination progenies Source-1 and polycross progenies	7	+ 0.06	+ 0.64
Open-pollination progenies Source-1 and open-pollination progenies Source-2	6	+ 0.73	+ 0.85
Parent clones and single cross averages	7	+ 0.21	+ 0.97**
Parent clones and open-pollination progenies	7	+ 0.35	+ 0.87**
Parent clones and polycross progenies	7	+ 0.80*	+ 0.74

* Significance P = 0.05.
** Significance P = 0.01.

The reliability of single plants as top-cross testers for a group of selections was obtained by a rearrangement of single cross data presented in Tables 1 and 2. Each of the seven bromegrass selections was in turn considered as a top-cross tester for the remaining six plants. When evaluating a plant as a tester all single crosses of it with other plants were extracted and considered as tester crosses. Single crosses of the remaining plants were then averaged to present new values with which tester crosses could be compared. When any plant was treated as a tester, crosses of this plant were not represented in the single cross average as this would have led to exaggerated correlations when tester and single crosses were compared.

As shown by the data in Table 5 there was little relationship between the yield of tester crosses and the average yield of single crosses. This indicates that the plants involved in these studies when used singly in top-crosses cannot be considered reliable testers of combining ability. It signifies in addition that specific combining ability or the particular yield response of a plant in a cross is not closely related to general combining ability or the average behaviour of the plant in crosses. For the creeping habit there was a much better relationship between the response of tester crosses and the average of single crosses and in three of the seven comparisons significant correlations were shown.

The relative importance of specific and general combining ability also was shown by the analysis of variance of single cross yields according to the method of Sprague and Tatum (25). In this method the general combining ability variance results from variation of the mean yields of crosses of parents about the mean yield of the test whereas specific combining ability variance arises from variations of the yields of particular crosses from the yields expected on the basis of average parental performance. As indicated in Table 6 specific combining ability was relatively more important than general combining ability. It would appear that

TABLE 5.—CORRELATION COEFFICIENTS FOR THE YIELD AND THE DEGREE OF CREEPING SHOWN BY TESTER CROSSES AND BY THE AVERAGE RESPONSE OF SINGLE CROSSES FOR SEVEN SELECTED PLANTS OF BROMEGRASS

Tester plant	n	Yield	Creeping habit
16	6	+ 0.27	+ 0.66
18	6	+ 0.28	+ 0.83*
19	6	+ 0.23	+ 0.80
83	6	− 0.73	+ 0.58
85	6	+ 0.56	+ 0.94**
87	6	− 0.42	+ 0.39
90	6	− 0.28	+ 0.82*

* Significance P = 0.05.
** Significance P = 0.01.

TABLE 6.—THE RELATIVE IMPORTANCE OF GENERAL AND SPECIFIC COMBINING ABILITY AS SHOWN BY THE YIELDS OF SINGLE CROSSES OF SEVEN NON-INBRED BROMEGRASS SELECTIONS

Selection	Variance	
	General combining ability	Specific combining ability
16	0.0	0.4760
18	0.1651	0.2032
19	0.0	0.5995
83	0.2395	3.8432
85	0.0	2.0050
87	0.4369	1.7312
90	0.3903	3.7307
Total	1.2318	12.5888

genes with epistatic and dominance effects are more important than genes with additive effects in determining the yields of these bromegrass crosses. Since the degree of crossing was uncertain in some crosses the high specific effects are in part the result of this factor.

The fact that certain selections were partially self-fertile tended to detract from the accuracy of comparisons for yields and creeping determinations but resulted in other observations of interest. The number of small plants was counted in all plots and used as an index of the number of selfed plants in different progeny classes. While classification of plants as selfs on the basis of size is open to serious criticism the method is thought reasonably reliable in this instance in view of the good correspondence of the number of selfed plants indicated by size and the number to be expected from tests of self-fertility of parents plants. Table 7 presents a summary of the percentages of small plants in progenies of selections and the fertility ratings of selections as shown by extensive tests in 1948.

There was a high percentage of small plants in controlled crosses in comparison with the percentages in open-pollination progenies and polycrosses. In addition, the percentages of small plants in all types of progenies bore a rather definite relationship to the self-fertility index of parent

TABLE 7.—PERCENTAGES OF SMALL (LIKELY SELFED) PLANTS APPEARING IN VARIOUS PROGENY CLASSES OF BROMEGRASS AND THE SELF- AND OPEN-FERTILITY RATINGS OF PARENT PLANTS AS SHOWN BY SEED SETTING DETERMINATIONS

Selection	Percentage of small plants				Fertility ratings*	
	Single crosses	Open-pollination progenies		Polycross progenies	Self	Open
		Source-1	Source-2			
16	5.4	1.5	1.5	0.0	2.9	59.2
18	10.0	1.5	1.5	1.5	1.7	9.3
19	1.2	0.0	1.5	0.0	1.1	48.0
83	11.4	3.0	3.0	7.6	12.8	45.3
85	56.4	9.1	—	6.0	22.1	66.6
87	14.4	1.5	0.0	1.5	2.2	45.8
90	1.1	1.5	3.0	6.0	1.1	34.9
Average	14.3	2.6	—	3.2	6.3	44.2

* Expressed in terms of seeds per panicle.

plants. Progenies of plant 85, for example, showed a relatively high percentage of small plants and this plant produced more seed on selfing than did any other plant. The percentages of small plants observed in open-pollination and polycross progenies were much below those expected from the self-fertility ratings of parent plants. Open-pollination progenies and polycross progenies on the average showed 2.6 per cent and 3.2 per cent small plants, respectively while the average set of seed on selfing was 14.2 per cent of the seed set under open-pollination. This suggests the existence of pollen selectivity under free pollination in the field and the possibility of obtaining a reasonably high percentage of crossing between moderately self-fertile plants under natural pollination conditions. Although the number of selected plants in this study was limited there was no indication that highly self-sterile plants gave higher yielding progenies than partially self-fertile plants as found by Tysdal and Kiesselbach (31) for alfalfa. The yields of open-pollination progenies and polycross progenies of plants 83 and 85 were not inferior to the yields of progenies of other less self-fertile selections.

Crested Wheatgrass (Fairway Type)

Non-inbred Material

The analysis of variance of forage yields for the test of non-inbred Fairway material indicated highly significant differences to exist between the 64 strains entering the test. The coefficient of variability for this trial was 17 per cent. Analysis as for a lattice design resulted in an efficiency of 147 per cent as compared to the randomized block design analysis. Average yields were adjusted for block effects and used for all subsequent comparisons of strains. Forage yields of single crosses, other types of progenies, and parent clonal lines are given in Table 8. Since single crosses were not reciprocal they are entered in Table 8, without regard to the direction in which crosses were made. As all plants of this group were highly self-sterile marked differences in the performance of reciprocal crosses were not expected.

TABLE 8.—AVERAGE YIELDS IN POUNDS GREEN WEIGHT PER PLOT OF SINGLE CROSSES, OPEN-POLLINATION PROGENIES, VARIETY TOP-CROSSES AND CLONAL LINES OF NINE SELECTED PLANTS OF FAIRWAY CRESTED WHEATGRASS (SIX-REPLICATE LATTICE TEST OF 64 STRAINS, PLANTED, JUNE 1947, HARVESTED, JULY 1948)

Selection	Single cross when selection in column one crossed with:								Single cross average	Open-poll. progeny	Variety top-cross	Clonal line
	23–7	23–9	23–12	23–14	23–25	30–16	35–4	35–10				
23–5	5.35	6.84	7.02	6.32	5.59	5.56	5.78	6.38	6.10	5.71	6.03	2.12
23–7		6.98	6.12	6.87	5.85	4.59	6.52	6.56	6.10	5.54	5.82	2.20
23–9			6.20	7.10	6.33	6.69	7.10	7.06	6.79	7.43	—	2.03
23–12				7.30	5.78	6.13	6.44	7.35	6.54	6.97	—	3.50
23–14					6.17	5.41	6.66	6.54	6.55	6.35	6.09	2.63
23–25						5.76	5.16	5.82	5.81	5.87	5.52	3.39
30–16							5.51	6.31	5.74	5.89	—	2.93
35–4								6.77	6.24	7.04	—	4.29
35–10									6.60	6.59	6.90	3.22
Average									6.27	6.38	—	2.92
Range									1.05	1.89	—	2.26
Check strains: S-39-$\bar{3}$-1												4.87
S-38-$\bar{9}$-1-3												4.98
S-32-$\bar{28}$-1-1												5.26
S-39-$\bar{7}$-1												4.90
Fairway												5.88

L.S.D.—means of 6 plots 0.95
means of 48 plots 0.34
means of 6 and 48 plots 0.72

Nine single crosses in this test significantly outyielded the Fairway variety. Most of these high-yielding crosses involved plants 23-9 or 23-12 which were selections whose open-pollination progenies also were high in yield. The highest yielding cross, 23-12 × 35-10, gave a yield of 7.35 pounds per plot as compared to a yield of 5.88 pounds per plot for the Fairway variety. The yield of this cross was still below that of the highest yielding open-pollination progeny of plant 23-9 which yielded 7.43 pounds per plot. Most of the low yielding crosses involved plants 23-5, 23-25, or 30-16 which were selections having low yielding open-pollination progenies. The average yield of all open-pollination progenies was slightly but not significantly above the average yield of all single crosses (minimum difference for significance at the 5 per cent level equals 0.25 pounds per plot).

The inter-relationships of yields for various progeny classes and clones are shown in Table 9 by means of correlation coefficients. The significant correlation coefficient of + 0.76 between the average yield of single crosses and the yield of open-pollination progenies indicates that these progeny types gave fairly comparable indices of the combining ability of selections. Correlations were not made between the yields of variety top-crosses and other types of progenies because of inadequate data. However, there appears to have been reasonably good agreement between the yields of top-crosses and open-pollination progenies (Table 8). The small discrepancies between the yields of these two progeny classes were not significant for any of the five selections on the basis of calculated least significant difference values. The non-significant coefficients of − 0.13 between parent clones and single crosses and + 0.32 between parent clones and open-pollination progenies were expected in view of the poor development of parent clones in 1947.

TABLE 9.—CORRELATION COEFFICIENTS OF FORAGE YIELDS OF SINGLE CROSSES, OPEN-POLLINATION PROGENIES, TESTER CROSSES, AND CLONAL LINES OF NINE SELECTED PLANTS OF THE FAIRWAY VARIETY OF CRESTED WHEATGRASS

Comparison	n	r
Single cross averages and open-pollination progenies	9	+ 0.76*
Single cross averages and tester crosses of plant 23–5	8	+ 0.78*
Single cross averages and tester crosses of plant 23–7	8	+ 0.72*
Single cross averages and tester crosses of plant 23–9	8	+ 0.15
Single cross averages and tester crosses of plant 23–12	8	+ 0.38
Single cross averages and tester crosses of plant 23–14	8	+ 0.70*
Single cross averages and tester crosses of plant 23–25	8	+ 0.41
Single cross averages and tester crosses of plant 30–16	8	+ 0.42
Single cross averages and tester crosses of plant 35–4	8	+ 0.86**
Single cross averages and tester crosses of plant 35–10	8	+ 0.72*
Parental clones and single cross averages	9	− 0.13
Parental clones and open-pollination progenies	9	+ 0.32

* Significance P = 0.05.
** Significance P = 0.01.

Each plant was considered as top-cross tester for the remaining plants of the group as has been described for bromegrass selections. When five of the selections were used as tester plants significant correlations were obtained between the yields of tester crosses and the average yield of single crosses. Apparently certain plants may be used for testing the combining ability of selections and be expected to give results comparable to those obtained from crossing selections with several plants. However, when plant 23-9 was used as a tester the yields of tester progenies showed a non-significant correlation of + 0.15 with the average yield of single crosses. This plant is specific in the manner in which it combined with other plants to give vigorous progenies. It is interesting to note that the average yield of single crosses and the yield of the open-pollination progeny of this plant were greater than the yields of comparable progenies of any other selection, that is, general combining ability was also high. Table 10 presents variance values for general and specific combining ability as determined by analysis of single cross yields according to the method of Sprague and Tatum (25). On the whole general and specific combining ability appear equally important in this group of selections since total variance values for each factor are similar. Selections 23-5, 23-14, 23-25, 35-4, and 35-10 show low specific combining ability variances. Except for 23-25 all of these plants when used as individual top-cross testers gave tester yields which correlated well with the average yields of single crosses (Table 9). These plants then would appear to be particularly suitable for testing the general combining ability of new selections in the breeding program.

Inbred Material

In the test of inbred plants of the Fairway type of crested wheatgrass the yields of clonal rows were extremely low and for this reason clonal lines were omitted from the analysis of variance and all subsequent considerations. The analysis of the remaining 42 strains indicated a highly significant difference between progenies for yield of green weight. The coefficient of variability for this test was 17 per cent. In calculating the average

TABLE 10.—THE RELATIVE IMPORTANCE OF GENERAL AND SPECIFIC COMBINING ABILITY FROM THE ANALYSIS OF SINGLE CROSS YIELDS INVOLVING NINE SELECTIONS OF FAIRWAY CRESTED WHEATGRASS

Selection	Variance	
	General combining ability	Specific combining ability
23–5	0.0253	0.0406
23–7	0.0253	0.2339
23–9	0.3297	0.1484
23–12	0.0804	0.2412
23–14	0.0829	0.0644
23–25	0.2735	0.0682
30–16	0.3550	0.2349
35–4	0.0	0.0260
35–10	0.1236	0.0
Total	1.2957	1.0576

yields of single crosses the yields of reciprocals were averaged and the single values obtained used for further averaging. However, in making correlations of the yields of tester crosses, single yields were taken at random from the reciprocal pair to represent the tester cross and to calculate the average single cross yield. This was done to allow the comparison of correlation coefficients on the basis of equal replication. Table 11 presents the yields of all strains included in this test and Table 12 shows correlation coefficients obtained by comparing the yields of different progeny classes and clonal lines.

Single crosses of this group of inbred plants showed a wide range in yield with the highest yielding cross producing 7.16 pounds and the lowest yielding producing 3.01 pounds of green weight per plot. Of the 30 single crosses only one, 41-17 × 44-19, significantly outyielded the Fairway check. On the other hand, nine crosses were significantly lower than the Fairway check in yield of forage. Six of these low yielding crosses included selection 43-15 which was self-fertile to a slight extent. Other low yielding crosses involved selections 41-13 and 43-17. Of the nine crosses present in reciprocal only the 41-17 x 43-15 cross showed a significant difference between the yield of the reciprocal members. The different yield of reciprocals in this case may be explained by the partial self-fertility of plant 43-15. As in the group of non-inbred plants discussed previously the average yield of all single crosses was slightly below the average yield of all open-pollination progenies but the difference was not significant. (Minimum difference for significance at the 5 per cent level equals 0.31 pounds per plot). The yield of the open-pollination progeny of plant 41-17 is particularly outstanding, being significantly higher than any other open-pollination progeny.

A significant correlation was found between the average yields of single crosses and the yield of open-pollination progenies (Table 12). This suggests that open-pollination progenies may be utilized to obtain a reliable index of combining ability. When individual plants were used as testers a significant correlation between the yields of tester crosses and the average

TABLE 11.—AVERAGE YIELDS IN POUNDS GREEN WEIGHT PER PLOT OF SINGLE CROSSES AND OPEN-POLLINATION PROGENIES OF SEVEN SELECTED INBRED PLANTS OF THE FAIRWAY TYPE OF CRESTED WHEATGRASS (SIX REPLICATE LATTICE TEST OF 49 STRAINS, SEEDLINGS PLANTED, JUNE 1947, HARVESTED, JULY 1948)

Selection	Inbred line	Self-fertility*	Yield of selection in column one when crossed with:						Single cross average	Open pollination progeny
			41–17	43–9	43–15	43–17	44–17	44–19		
41–13	A	0.5	— 5.14	5.05** 5.91	3.76 3.01	4.73 —	— 4.89	4.63 5.12	4.75	5.11
41–17	A	0.0		6.06 6.88	6.70 3.37	6.88 6.61	6.58 6.00	7.16 6.23	6.06	6.68
43–9	B	0.0			5.98 —	5.11 —	5.55 —	6.60 —	5.86	5.49
43–15	C	5.2				3.09 —	— 3.97	3.98 —	4.24	4.84
43–17	C	0.0					4.83 —	4.98 5.81	4.98	5.13
44–17	D	0.0						4.95 —	5.08	5.14
44–19	D	0.0							5.42	5.22
Average									5.20	5.37
Range									1.82	1.84
Check strains—S-39-3-1										4.82
S-38-9-1-3										4.32
S-32-28-1-1										5.45
S-39-7-1										5.20
Fairway										5.91

L.S.D.—means of 6 plots 1.04
means of 36 plots 0.42
means of 6 and 36 plots 0.80

* In terms of seeds per spike.

** The upper value in each cell indicates the yield of the cross when the selection in column 1 was the female parent i.e. 41-13 × 43-9. The lower value indicates the yield of the cross when the selection in column 1 was used as the male parent i.e. 43-9 × 41-13.

TABLE 12.—CORRELATION COEFFICIENTS FOR FORAGE YIELDS OF SINGLE CROSSES, OPEN-POLLINATION PROGENIES, AND TESTER CROSSES FOR SEVEN INBRED PLANTS OF THE FAIRWAY TYPE OF CRESTED WHEATGRASS

Comparison	n	r
Single cross averages and open-pollination progenies	7	+ 0.81*
Single cross averages and tester crosses of plant 41–13	6	+ 0.83*
Single cross averages and tester crosses of plant 41–17	6	+ 0.26
Single cross averages and tester crosses of plant 43–9	6	+ 0.48
Single cross averages and tester crosses of plant 43–15	6	+ 0.91*
Single cross averages and tester crosses of plant 43–17	6	+ 0.80
Single cross averages and tester crosses of plant 44–17	6	+ 0.93**
Single cross averages and tester crosses of plant 44–19	6	+ 0.98**

* Significance P = 0.05.
** Significance P = 0.01.

yield of single crosses was obtained for four of the seven plants. Selections 41-17 and 43-9 gave results in tester crosses which correlated poorly with the average response of single crosses. This indicates that these selections were selective in the manner in which they combined with other plants. As was observed in the intercrosses of non-inbred plants of the Fairway type those selections showing a high degree of specific combining ability gave high yielding single crosses and open-pollination progenies.

The relative importance of general and specific combining ability variances as shown by single cross yields is given in Table 13. On the whole, the performance of selections in single crosses appears to have been determined more by the general reaction than by specific effect. These results are in agreement with those of Sprague and Tatum in corn (25) where general combining ability was found to be relatively high in inbred lines not selected previously for combining ability. Selections 44-17 and 44-19 appear suitable for testers of general combining ability in view of the low specific variances noted here for their crosses.

TABLE 13.—THE RELATIVE IMPORTANCE OF GENERAL AND SPECIFIC COMBINING ABILITY SHOWN BY SINGLE CROSSES INVOLVING SEVEN INBRED SELECTIONS OF FAIRWAY CRESTED WHEATGRASS

Selection	Variance	
	General combining ability	Specific combining ability
41–13	0.4378	0.4455
41–17	1.9668	0.7255
43–9	0.7245	0.4310
43–15	0.9612	0.7167
43–17	0.1483	0.3692
44–17	0.0	0.0427
44–19	0.0	0.0
Total	4.2386	2.7306

Three single crosses arose from the intercrossing of sister plants of the same inbred lines. An inspection of Table 11 will reveal that the yields of these sib-crosses were not conspicuously lower than the yields of out-crosses of these plants with non-related plants. The yield of the cross 41-17 × 41-13 was intermediate between the average yields of single crosses of the parent plants. The cross 43-15 × 43-17 was low yielding but this may have resulted from the occurrence of selfed plants in the cross as the 43-15 parent was partially self-fertile. The yield of the third cross of related plants, 44-17 × 44-19, was very similar to the average yield of the single crosses of either parent.

Crested Wheatgrass (Standard Type)

The test of seven selections of Standard crested wheatgrass was similar to those for the other species. Ten of the 21 possible single crosses were reciprocal but marked differences in reciprocal performance were not anticipated in view of the high self-sterility of parent plants. The analysis of variance for forage yields indicated a significant difference among the

49 entries involved in the test. The coefficient of variability was 13 per cent. Efficiency when analysed as a lattice test as compared with that when analysed as a randomized block test was 119 per cent. Average yields were corrected for block effects and the corrected yields used for all subsequent comparisons. Table 14 indicates the average yields of all strains included in this test. The method of averaging the yields of single crosses was similar to that described previously for crosses of inbred plants of the Fairway type.

TABLE 14.—AVERAGE YIELDS IN GREEN WEIGHT PER PLOT OF SINGLE CROSSES, OPEN-POLLINATION PROGENIES, AND CLONAL LINES OF SEVEN SELECTED PLANTS OF THE STANDARD TYPE OF CRESTED WHEATGRASS (SIX-REPLICATE LATTICE TEST OF 49 STRAINS, SEEDLINGS PLANTED, JUNE 1947, HARVESTED, JULY 1948)

Selection	Self-fertility*	Single cross when selection in column one crossed with:						Single cross average	Open-pollination progeny	Clonal line
		14–3	14–19	14–20	14–34	19–9	19–16			
14–2	0.1	6.06** / 6.37	7.44 / —	6.15 / 6.62	— / 6.51	6.02 / 6.25	— / 5.80	6.41	6.15	4.65
14–3	0.2		6.05 / 7.84	6.90 / 7.23	— / 6.41	6.29 / 6.60	5.77 / 6.50	6.54	7.65	6.06
14–19	0.0			— / 8.35	6.75 / 7.68	8.53 / —	7.46 / 7.00	7.62	8.81	4.42
14–20	0.1				7.41 / —	8.13 / —	— / 7.22	7.43	7.23	5.6
14–34	0.0					7.48 / 7.24	— / 5.56	6.74	6.82	4.67
19–9	0.2						— / 7.01	7.27	7.76	7.70
19–16	0.6							6.49	6.58	4.22
Average yield								6.93	7.29	5.34
Range in yield								1.21	2.66	3.48
Check strains—S-1333										6.82
Standard (U.S.D.A.)										6.56
S-131										6.41
Forage										7.20

L.S.D. (P = 0.05)—means of 6 plots 0.94
means of 36 plots 0.38
means of 6 and 36 plots 0.71

* Expressed in terms of seeds per spike.
** The upper value in each cell indicates the yield of the cross when the selection in column 1 was used as the female parent, i.e. 14-2 × 14-3. The lower value indicates the yield of the reciprocal cross, 14-3 × 14-2.

A survey of Table 14 indicates good correspondence in the yields of reciprocal crosses. Only in the cross 14-3 × 14-19 was there a significant difference between the yields of reciprocal pairs. As both parents of this cross were highly self-sterile such a difference between reciprocal crosses was not expected. Two crosses, 14-20 × 14-19 and 14-19 × 19-9, were significantly higher in yield than the Forage strain which was the check

most representative of the commercial lot from which original selections were made. These crosses both concerned plant 14-19 which on the basis of the average yield of single crosses or open-pollination progeny was the selection giving the highest yielding progenies of all the group. Eight crosses were significantly lower in yield than the Forage check and these crosses in most cases included plants 14-2 or 19-9. These plants, according to the average response of single crosses and open-pollination progenies were plants with low combining ability.

The greatest range in yield occurred among parent clonal lines. The parent clones had a range of 3.48 pounds per plot compared with a range of 2.97 pounds for individual single crosses, 2.66 pounds for open-pollination progenies, and 1.21 pounds for the average yields of single crosses. The average yield of 7.29 pounds per plot for all open-pollination progenies was significantly above the average yield of 6.93 for all single crosses. (Minimum difference for significance at the 5 per cent level equals 0.28 pounds per plot). The lower yield for single crosses conceivably may have arisen due to the presence of small numbers of selfed plants of inferior vigour within them. It is also possible that under open-pollination the original selected plants were subjected to more favourable sources of pollen than available within this relatively restricted group. The average yield of clonal lines was low in comparison with seedling material thus indicating the extent to which clonal material failed to become well-established.

Differential damage to strains for infestations of the western wheat aphis (*Brachycolus tritici* Gill.) was noted in this test and all strains were scored for resistance to damage. A score of 1 represented very severe effects and a score of 10 no injury. The analysis of variance of damage scores indicated a highly significant difference among strains with a coefficient of variability of 14 per cent. Analysis of damage by lattice methods resulted in an efficiency of 196 per cent as compared to the use of randomized block methods. The marked gain in efficiency from lattice methods indicates that infestation in the test area was localized to a high degree. In Table 15 the average resistance to aphis scores for all strains are shown along with self-fertility ratings of the seven parent selections.

Crosses differed greatly in their resistance to the western wheat aphis and in general were less affected than the check Forage strains. Original selections, however, were not selected in this respect. Four of the ten pairs of reciprocal crosses showed significant differences in aphis damage between reciprocals. Parent plants of these crosses were highly self-sterile and differences between reciprocals were not anticipated. It will be observed, however, that in the four crosses where reciprocals differed in reaction the reciprocal member with the lower score arose from the use of the lower reaction parent as female. Apparently selfing was occurring to a higher degree than was anticipated on the basis of tests of self-fertility in parent selections. One of the crosses, 14-34 × 19-9, exhibited almost complete resistance to damage with an average score of 9.88. The most severely damaged cross was 14-2 × 14-3 with a score of 4.61. Both parents of this cross were low in resistance to aphis attack. Open-pollination progenies were significantly less affected than single crosses and

TABLE 15.—REACTION SCORE TO THE WESTERN WHEAT APHIS (*Brachycolus tritici* GILL.) OF SINGLE CROSSES, OPEN-POLLINATION PROGENIES, AND CLONAL LINES OF SEVEN SELECTED PLANTS OF THE STANDARD TYPE OF CRESTED WHEATGRASS. (STRAINS SCORED FROM 1 TO 10 FOR REACTION)

Selection	Self-fertility*	Single cross when selection in column one crossed with:						Single cross average	Open-pollination progeny	Clonal line
		14–3	14–19	14–20	14–34	19–9	19–16			
14–2	0.1	4.61** 5.87	8.05 —	6.42 8.27	— 6.54	7.19 7.98	— 6.31	6.84	7.53	6.85
14–3	0.2		7.65 9.10	7.18 8.55	— 7.84	7.48 7.56	7.99 7.52	7.43	7.96	9.18
14–19	0.0			— 9.25	8.01 8.66	9.38 —	7.97 8.06	8.57	8.97	7.93
14–20	0.1				9.18 —	9.61 —	— 8.98	8.70	9.79	9.79
14–34	0.0					9.88 9.07	— 7.71	8.18	9.21	9.58
19–9	0.2						— 8.05	8.60	8.94	9.98
19–16	0.6							7.80	7.85	9.40
Average resistance								8.02	8.61	8.96
Range in resistance								1.86	2.26	3.13
Check strains—S-1333										8.43
Standard (U.S.D.A.)										8.11
S-131										9.09
Forage										6.97

L.S.D. (P = 0.05)—means of 6 plots 1.14
means of 36 plots 0.46
means of 6 and 36 plots 0.87

* Expressed in terms of seeds per spike.

** Upper value in each cell indicates the resistance of the cross with the selection in column 1 as the female parent, i.e. 14-2 × 14-3. Lower value indicates the resistance of the reciprocal cross, i.e. 14-3 × 14-2.

TABLE 16.—CORRELATION OF FORAGE YIELDS AND APHIS REACTION OF SINGLE CROSSES, OPEN-POLLINATION PROGENIES, TESTER CROSSES, AND CLONAL LINES FOR SEVEN PLANTS OF THE STANDARD TYPE OF CRESTED WHEATGRASS

Comparison	n	r	
		Yield	Aphis reaction
Single cross averages and open-pollination progenies	7	+ 0.77*	+ 0.89**
Single cross averages and tester crosses of plant 14–2	6	+ 0.63	+ 0.91*
Single cross averages and tester crosses of plant 14–3	6	+ 0.51	+ 0.79
Single cross averages and tester crosses of plant 14–19	6	+ 0.74	+ 0.84*
Single cross averages and tester crosses of plant 14–20	6	+ 0.92**	+ 0.95**
Single cross averages and tester crosses of plant 14–34	6	+ 0.83*	+ 0.88*
Single cross averages and tester crosses of plant 19–9	6	+ 0.88*	+ 0.86*
Single cross averages and tester crosses of plant 19–16	6	+ 0.86*	+ 0.76
Parental clones and single cross averages	7	+ 0.28	+ 0.70
Parental clones and open-pollination progenies	7	+ 0.28	+ 0.64

* Significance P = 0.05.
** Significance P = 0.01.

apparently less than clonal lines although the difference was not significant. Check strains varied greatly in aphis reaction with the Forage strain showing more damage than the other three strains.

Correlation coefficients given in Table 16 indicate that there was good agreement between the yields of open-pollination progenies of selections and the average yields of single crosses ($r = +0.77$). The yields of tester crosses also correspond well with the average yields of single crosses. Correlation coefficients ranged from $+0.51$ to $+0.92$ and in four of the seven tester cross comparisons were significant. A non-significant correlation coefficient of $+0.28$ was obtained from the comparison of clonal lines and single crosses and also for the comparison of clonal lines and open-pollination progenies. Since the development of clonal material in this test was rather satisfactory these correlation coefficients may be considered reasonably reliable. There was a close relationship also between the aphis reaction for single crosses and open-pollination progenies ($r = +0.89$). The response of tester crosses was very similar to the average response of single crosses and in five of the seven comparisons of these two classes of progenies significance was established. Between parent clonal lines and single crosses and between clonal lines and open-pollination progenies there were indications of rather high positive relationships but significance was not shown in either case.

TABLE 17.—THE RELATIVE IMPORTANCE OF GENERAL AND SPECIFIC COMBINING ABILITY FROM SINGLE CROSSES INVOLVING SEVEN STANDARD CRESTED WHEATGRASS PLANTS

Selection	Variance	
	General combining ability	Specific combining ability
14–2	0.3299	0.2376
14–3	0.4120	0.2466
14–19	0.5181	0.2556
14–20	0.4917	0.0
14–34	0.0	0.0742
19–9	0.2086	0.1498
19–16	0.3514	0.0482
Total	2.3117	1.0120

Table 17 gives variance values associated with specific and general combining ability as determined from the yields of single crosses for the seven Standard wheatgrass plants. The total variance for general combining ability is more than double that arising from specific combining ability. This contrasts with the group of non-inbred Fairway selections where the two variances were more or less comparable. Selections 14-20 and 19-16 showed low specific combining ability reactions and would appear most suitable as testers for general combining ability of new selections.

DISCUSSION

Sufficient inter-plant variation in combining ability was exhibited by commercial strains of bromegrass and crested wheatgrass to warrant the general selection of plants in open-pollinated strains on a combining ability basis. Three of the nine plants of the Fairway variety of crested wheatgrass and one of the seven plants of the Standard type were significantly superior to parent strains according to the yields of open-pollination progenies of these plants. None of the seven plants of bromegrass produced open-pollinated progenies which significantly outyielded the parent variety. Significant differences between the yields of progenies were noted, however. Doubtless the exploration of larger populations of these species would reveal a greater range of combining ability among plants and thus provide the possibility of more critical selection.

The relationship of combining ability shown by open-pollination progenies to that exhibited by single crosses was of primary concern in these studies. Interest in this regard arose from the current practice at the Dominion Forage Crops Laboratory of evaluating selections of bromegrass and crested wheatgrass almost entirely on the basis of open-pollinated progeny performance. Controlled single crosses were used as a standard for comparison as this kind of progeny results from a high degree of pollen control except that self-pollination may occur. Polycross progenies also would have formed a desirable standard for the comparison of selections but such progenies were not available for most of the selections tested. The fact that significant correlation coefficients of $+0.76$, $+0.81$, and $+0.77$ were found between the yields of open-pollination progenies and controlled crosses in the three tests of crested wheatgrass appears to justify the practice of selecting crested wheatgrass plants on the basis of open-pollination progeny performance. Lower, non-significant correlation values of $+0.44$ and $+0.68$ between the yields of open-pollination progenies and controlled crosses in bromegrass were attributed to the inclusion in crossed progenies of selfed plants. Had completedly self-sterile plants been used in the study on bromegrass it is possible that correlations as high as those found in crested wheatgrass would have been obtained. The significant correlations found between open-pollination progenies and those from controlled crosses with regard to the creeping character in bromegrass and the aphis reaction character in Standard crested wheatgrass appear to support the reliability of open-pollination progenies for testing parental breeding characteristics.

Seed for the production of open-pollination progenies can be harvested from selected plants in space-planted nurseries with a very minimum of effort. At this station sufficient seed commonly is obtained from single plants of bromegrass and crested wheatgrass to permit the planting of replicated plot tests or row tests. Where large numbers of selections are to be tested or small amounts of seed are available single unreplicated plots or rows might be sown with frequent checks of standard varieties for

comparison. Where comprehensive tests or regional trials are required clonal nurseries of selections would need to be established for selections to produce sufficient seed. Replication and randomization of clones in such nurseries would seem desirable to ensure the pollination of clones with random sources of pollen. In view of the reliability of open-pollination progenies in these studies it would appear that the isolation of such clonal material as recommended by Tysdal and associates (30, 31) for alfalfa is unnecessary and that extensive replication of clones in the clonal nursery may be unwarranted.

Tester crosses made by crossing selections with a single tester plant did not appear wholly satisfactory for testing the general combining ability of selections. In bromegrass the yields of tester crosses of selections did not correlate well with the average yields of more extensive crosses of such selections. Unfortunately the presence of self-fertility in certain bromegrass selections hindered interpretation. In crested wheatgrass approximately half of the plants appeared suitable as testers since the yields of tester crosses involving them were in agreement with the average yields of selections in several single crosses.

Comparisons of the yield variance of single crosses attributable to specific and general combining ability indicated that general combining ability was more important in crested wheatgrass. Specific combining ability appeared relatively more important in bromegrass but the contamination of crosses with selfed plants was responsible for part of this effect. Sprague and Tatum (25), Green (7), and Keller (13) pointed out the specificity of inbred lines and non-inbred plants of corn and noted that the maxium productivity of crosses could be obtained only when the specific reaction was considered. The specific combining ability shown by certain plants of crested wheatgrass is worthy of consideration when composite strains are formed from these plants. Where the composite involves few plants and ultimate production is wanted it would appear necessary that all plants forming the composite perform well in specific combinations with one another.

It was expected that within controlled single crosses certain fortuitous combinations would be found whose yields and plant type would merit an F_1 hybrid program with parents of crosses being increased vegetatively. Certain crosses indicated some hope for such a program. The highest yielding cross of bromegrass yielded 112 per cent of the parent variety Superior. In the Fairway type of crested wheatgrass highest yielding crosses in non-inbred and inbred material yielded 125 per cent and 121 per cent, respectively, of the Fairway check. The highest yielding cross in the Standard type of crested wheatgrass yielded 118 per cent of the Forage check. It is worth noting, however, that the yields of the best open-pollination progenies for these same four groups also were promising being respectively 109, 126, 113, and 122 per cent of check strains for the four groups. This would suggest that initially a hybridization plan might consist of growing single clonal lines in combination with seeded material of current varieties or other strains.

Since inbred and non-inbred materials were available for the Fairway type of crested wheatgrass it was possible to compare in a general manner the frequencies of plants with high combining ability in each group. Critical

comparisons were not possible since inbred and non-inbred progenies were tested in different areas of the experimental field and since inbred plants were not related to non-inbred plants. Of the nine non-inbred plants tested the average yields of single crosses for seven were above the yield of the Fairway check with significance being shown in two comparisons. In contrast only one of the seven inbred plants tested gave an average single cross yield above that of the Fairway check with significance not being shown. Tests of combining ability made from 1944 to 1947 in the general crested wheatgrass breeding program at Saskatoon also indicated that plants with superior combining ability occurred as frequently in non-inbred as in inbred strains. The average yield of open-pollination progenies of 102 selfed plants in lines inbred from one to three generations was 98.4 per cent of the Fairway check. The average yield of open-pollination progenies of 31 non-inbred selections was 105.3 per cent of the Fairway check. Of seven plants whose progeny yields were significantly above those of the check, four plants represented inbred lines and three represented non-inbred strains. In view of the high self-sterility of crested wheatgrass and the failure of inbreeding to augment the proportion of selections with improved combining ability it would appear that selfing as a breeding practice to improve the yield of this grass is not particularly promising.

Indications of the heritability of yield and other characters have been provided by correlation analyses between parent clones and progeny classes. A more suitable measure of the inheritance of plant characters is provided by progeny parent regressions with regression coefficients being doubled to provide heritability values (Lush 17). While such a method presumes controlled crossing of selections with common male parentage the technique appears appropriate for polycross and open-pollination progenies where pollination is more or less random. In brome the regression coefficients of the yield of controlled crosses, open-pollination progenies, and polycross progenies on the yield of parent clones were 0.06, 0.17, and 0.11, respectively. Significance ($P = 0.05$) was shown only for the regression of polycross progenies on parent clones. Similar regression coefficients for the degree of creeping of progenies were 0.42, 0.59, and 0.43 for controlled crosses, open-pollination progenies, and polycross progenies, respectively. In this instance all regressions were significant. In the Standard type of crested wheatgrass regression coefficients for progeny yields on parent yields were 0.11 for controlled crosses and 0.20 for open-pollination progenies. Coefficients of 0.51 for controlled crosses and 0.56 for open-pollination progenies were obtained for the regression of aphis reaction of progenies on the aphis reaction of parents. Significance was not shown for any of these regressions. Lower regressions noted for yield than for the creeping character in bromegrass and the insect resistance character in crested wheatgrass indicate the relatively greater need of progeny testing where yield is being studied. Tsiang (29) also noted a lower correlation of selfed lines and clones in bromegrass where comparisons involved yield of forage than where comparisons concerned disease resistance, degree of creeping, and plant height.

The reasonably high regressions of progenies on parent for the degree of creeping in bromegrass is an indication that despite the high-polyploid nature of the species and the irregularity of meiosis as shown by Elliott and

Love (5) there is nevertheless rather stable inheritance for certain characters. Unfortunately, reliable correlations were not available for parent-progeny yield comparisons in Fairway crested wheatgrass; otherwise correlations on diploid, tetraploid, and octoploid levels would have been possible. While the species are different the comparison of the Standard type of crested wheatgrass and bromegrass indicates no marked difference to exist in the general heritability of characters between the tetraploid and octoploid levels.

All comparisons in these studies involved plants growing under space-planted conditions. It is possible that observed differences between strains might have been reduced had plants been growing under conditions of mass seeding. Single crosses containing admixtures of plants arising from selfing likely would have yielded more favourably under mass seeded conditions as a result of the suppression of the smaller selfed plants by crossed plants. The comparative yields of bromegrass and crested wheatgrass under nursery and mass seeded conditions have been studied at this laboratory and moderately good correspondence has been observed. Two composite strains have been formed by grouping clones of the better Fairway and Standard parent selections in these studies. The performance of these composite strains should provide an additional index of the reliability of combining ability procedures which have been recommended.

SUMMARY

1. Studies of combining ability were conducted with single open-pollination plants of commercial strains of bromegrass, Fairway crested wheatgrass, and Standard crested wheatgrass, and for inbred plants of the Fairway type of crested wheatgrass. Combining ability of plants was measured by the forage production of progenies of various types, including controlled single crosses, open-pollination progenies, and in certain cases polycross and top-cross progenies.

2. Significant differences in combining ability were noted among plants of the four groups of plants studied. Three of the nine plants of the Fairway variety of crested wheatgrass and one of the seven of a commercial lot of the Standard type produced open-pollination progenies which out-yielded the parent strain. The combining ability of inbred plants of Fairway crested wheatgrass varied between and within inbred lines but the merit of inbred plants as parents was below that of non-inbred material.

3. Open-pollination progenies of selected plants gave indices of combining ability in agreement with those of controlled crosses in crested wheatgrass but not in bromegrass. Correlation coefficients of the two classes of progenies were $+0.76$, $+0.81$ and $+0.77$ in non-inbred Fairway, inbred Fairway and Standard crested wheatgrass, respectively. In bromegrass non-significant correlation coefficients of $+0.44$ and $+0.68$ were obtained between the yields of controlled crosses and open-pollination progenies derived from duplicate field sources. The lower correlations in bromegrass were considered to result largely from the contamination of controlled cross progenies with selfed plants.

4. Where polycross progenies were available in bromegrass the yields showed a low relationship to the yields of controlled crosses. In the

Fairway type of crested wheatgrass the combining ability ratings for five selections as shown by the yields of variety top-crosses were not significantly different from those shown by the yields of controlled crosses.

5. Single plants appeared quite variable in their reliability as top-cross testers of combining ability. Approximately half of the plants in each of the three groups of crested wheatgrass gave top-cross progeny yields which were significantly correlated with the yields of controlled crosses of these selections. In bromegrass none of the selections was satisfactory as a top-cross tester for other selections.

6. Highly significant correlation coefficients of $+0.88$ and $+0.94$ were noted in bromegrass between the degree of creeping of open-pollination progenies and the degree of creeping shown by controlled crosses of the same parent plants. In the Standard type of crested wheatgrass a highly significant correlation of $+0.89$ was found between the aphis resistance of open-pollination progenies and that shown by single crosses.

7. In both bromegrass and the crested wheatgrasses little relationship was found between the yields of parent clones and their progeny classes. This fact emphasizes the importance of using progeny rather than clonal lines in the evaluation of plants of these grasses for yielding potential. Significant correlations were found between parent clones and progenies in respect to the creeping rooted character in bromegrass and the reaction to aphis character in crested wheatgrass.

8. The results obtained appear to justify the current breeding practice of confining selection to plants of open-pollinated populations or crossed populations and also the evaluation of selections on the basis of open-pollination progeny performance. Since certain plants were highly specific in the manner in which they combined with other selections to give vigorous progenies it would seem necessary to consider the specific response of selections when plants were composited to form new strains.

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A STUDY OF THE HOT WATER TREATMENT OF BARLEY FOR THE CONTROL OF LOOSE SMUT, *USTILAGO NUDA*[1]

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The hot water treatment was first evolved in 1887 by Jensen (13) in Denmark, as a control for smut diseases in general. Since then it has been studied and modified by various workers. Appel (5) used the treatment for the specific purpose of controlling the loose smut of wheat and barley. He emphasized the importance of pre-soaking the seed for a definite period of time at a definite temperature. He believed that pre-soaking the seed broke the dormancy of the mycelium of the parasite so that it could be destroyed more easily by heat. Tapke (16) pointed out the marked influence that cracks in the seed coat have upon damage to the seed from the hot water treatment. He also described methods for applying the treatment on a large scale. Gassner (7) and Gassner and Kirchhoff (8, 9) proposed treating the seed in closed containers. They stated that, under these conditions, intra-molecular respiration took place, with the formation of alcohol and other cleavage products. They considered that these were largely responsible for the control of the disease, and stated that they obtained better results by adding a little alcohol to the water in which the grain was soaked. Dieudonne and Vanderwalle (6) reported that treating barley seed for 20 minutes at 128° F. was ineffective when the seed was not pre-soaked.

It is very important that the seed of promising new varieties, if it carries any loose smut infection, should be freed from this infection before the seed is increased and distributed to farmers. Ordinarily, only the more valuable barley seed is subjected to the hot water treatment, and heavy damage to such seed is a matter of more importance than would be the destruction of an equal amount of ordinary seed. At the commencement of the studies reported below, it was found that the standard schedule, recommended in Canadian Government pamphlets (1, 2) for the application of the hot water treatment to barley seed, destroyed the viability of a considerable portion of the seed, and that the schedule recommended in Leaflet No. 1, Supplement No. 2, of the War Service Committee of the Upper Mississippi Valley Plant Pathologists (3), was even more injurious. Therefore it was decided that the hot water treatment should be investigated under present day conditions in the Prairie Provinces with a view to controlling loose smut with as little injury as is feasible to the seed.

MATERIAL AND METHODS

Barley seed from different places in Saskatchewan, naturally infected with loose smut (*Ustilago nuda* (Jens.) K. & S.), was used in all tests where the plants were raised to the flowering stage and the infection recorded. Spores from representative diseased heads were germinated on agar to make sure that the parasite present was not *U. nigra* Tapke. In germination tests involving only the seedling stage, uninfected seed of varieties commonly grown in Saskatchewan was sometimes used.

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The following method was employed in heating the seed. An electric warming plate with the heating coil under one end gave the required amount of heat for the purpose. The seed was placed in hot water in a glass beaker set inside a slightly larger one, so that the seed did not come in contact with a glass surface resting directly on the hot plate. The beakers could be placed directly over the heating unit or moved away from it, thus securing the temperature desired. While the seed was in the hot water bath, it was stirred with a thermometer. When necessary the temperature of the bath was adjusted by adding hot or cold water.

In larger scale treatments, the seed was placed in baskets made of strap metal frames and copper wire screening, and dipped into water heated with live steam in a concrete tank. The baskets were forced up and down in the hot water bath and the seed was thus spread apart and the water passed through it rapidly so that the seed was all heated at a uniform rate. The temperature of the water was checked constantly with a thermometer and adjusted by passing live steam into the tank.

In those tests designed to show the amount of seed injury as reflected in lower percentage germination, the seed was sown in soil in wooden flats. Three hundred seeds were used for each treatment and this number was sown in each flat. About ten days later, the seedlings were harvested and the percentage that had emerged was computed.

In experiments in which the plants were to be grown to maturity, the seed was sown in soil in one-gallon crocks, for most of the greenhouse tests, and in eight-foot rows for field tests. In the greenhouse tests, four crocks, each sown with about 27 seeds, were devoted to each treatment. In the field tests, about 110 seeds were sown in each row and four or five replications were used. When these tests were harvested, the number of healthy and smutted heads was recorded.

EFFECTS OF VARIATIONS IN THE DIFFERENT STEPS OF THE HOT WATER SCHEDULE ON THE GERMINATION OF BARLEY

The various steps of the hot water treatment schedule were investigated successively to study their separate effects on the germination of the seed. This was done to discover what factors were responsible for most of the reduction in viability.

The first step is the pre-soaking of the seed. In one test three different samples of barley were each divided into six portions, and, after these were pre-soaked at room temperature for periods of time ranging from nil to 25 hours, they were sown without being treated with hot water. It was found that there was no significant difference in the percentage germination of the different portions.

In a second test three samples were each divided into five portions. One portion was neither pre-soaked nor treated and it served as a check. One portion was treated without being pre-soaked, and the remaining portions were pre-soaked for 5, 10, and 20 hours before being treated for 11 minutes at 126° F. (see Figure 1). On the average, treatment without pre-soaking reduced germination by only 3 per cent; but after a 5-hour pre-soak, followed by treatment, it was reduced 20 per cent; after a 10-hour pre-soak, 59 per cent; and after a 20-hour pre-soak, 78 per cent, as compared with the untreated check.

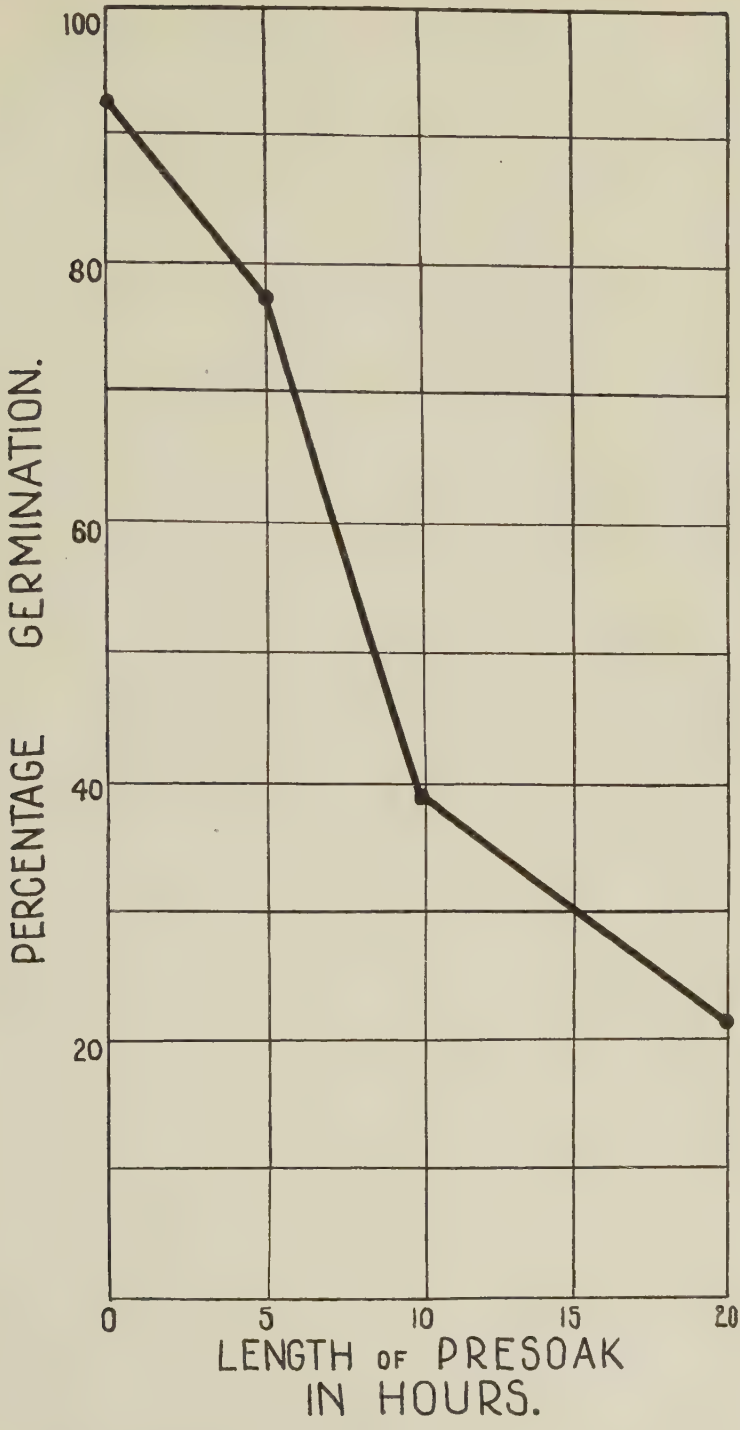

FIGURE 1. The effect of the length of time that the seed is pre-soaked on the germination of treated barley seed.

As a long period of pre-soak caused such severe injury to the seed, it was decided to study the effect of shorter periods of pre-soaking. For a third test, five samples of Montcalm barley were each divided into four portions. Besides the check, which was neither pre-soaked nor treated, one portion was pre-soaked for two hours at room temperature, another for three hours, and a third for four hours, followed by the usual hot water bath. In this test, the average germination of the checks was 95 per cent. When pre-soaked for two hours and treated, the seed had an average germination of 90 per cent; three hours, 86 per cent; and four hours, 79 per cent.

The results of the first test showed that pre-soaking even for relatively long periods, when not followed by the hot water bath, did not depress germination appreciably. In the second test the application of the hot water treatment for 11 minutes at 126° F. had very little effect on the viability of the seed when it was not pre-soaked; but in both the second and third tests, losses in viability increased regularly with each increase in the length of the pre-soak period when these were followed by the hot water bath.

The next step in the hot water treatment is the exposure of the seed to heat in the water bath. Three samples of barley belonging to the following varieties were used: Newal, Plush, and Vantage. Different portions of each sample were pre-soaked for five hours at room temperature and then dipped for 11 minutes in water baths ranging from 120° F. to 130° F. at two-degree intervals (see Figure 2). The average germination of the treated samples varied from 94 per cent, when the treating temperature was 120° F., to 14 per cent, when the temperature was 130° F. The average germination of the untreated checks was 97 per cent. At 126° F., it was 73 per cent and, at 128° F., 48 per cent.

Some reduction in germination took place after treatment at all the temperatures used. The hot water treatment not only reduced the percentage germination, but also retarded germination quite noticeably and tended to weaken the seedlings during the early stages of growth. The rapidity with which the damage to the seed increased at temperatures above 124° F. emphasizes the desirability of treating at the lowest temperature that will insure the control of the disease.

The third step in the hot water treatment, which admits of considerable variation, is the period of time elapsing between treating and sowing. The seed of four different samples of barley was used for this test, and each sample was divided into five lots of 300 kernels immediately after the hot water treatment was applied. In this experiment, all portions of each sample were pre-soaked and treated with hot water in the same manner. After the hot water treatment, the different lots were dried at room temperature for periods of 1, 5, 10, 15, and 20 days, and then sown. There were no marked differences in the average percentage germination of these different lots, although in each instance the lot dried for 5 days germinated slightly better than the ones dried for 1 day, or those dried for 10, 15, or 20 days.

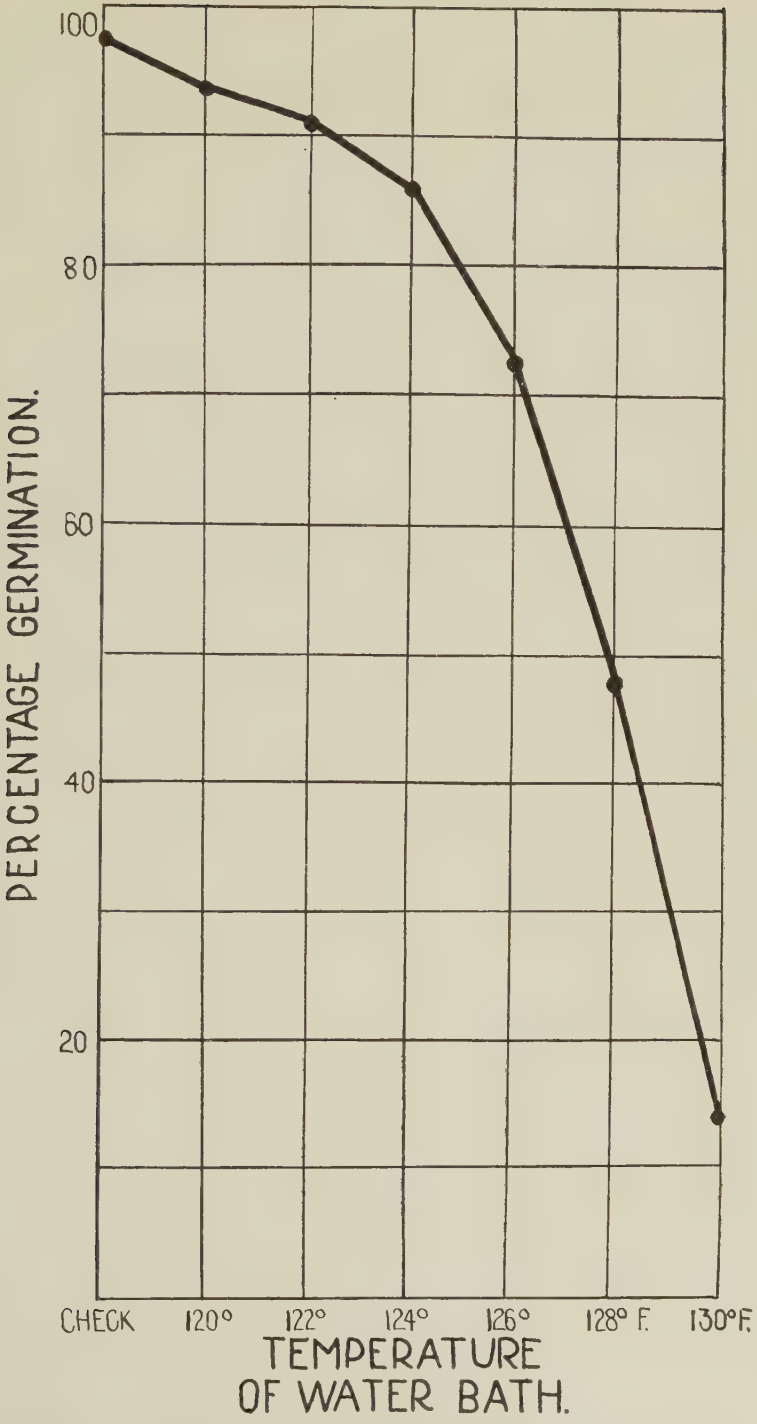

FIGURE 2. The effect of the temperature of the water bath on the germination of treated barley seed.

INFLUENCE OF BROKEN SEED-COATS ON DAMAGE TO THE SEED FROM THE HOT WATER TREATMENT

Besides the studies on the separate effect of each step in the hot water treatment, the effect of mechanical injuries to the barley seed was investigated. Samples of three different varieties of barley were each divided into three portions. One portion was threshed just once, the second was run through the threshing machine three times and the third portion, six times. Then the hot water treatment (pre-soaked 6 hours at 70° F.; dipped 11 minutes at 126° F.) was applied to one-half of each lot, and the other half was sown without treatment.

The effect of repeated threshing was to reduce the percentage germination of the untreated as well as the treated seed. After being threshed once, the untreated seed had an average germination of 89 per cent; after three times, 84 per cent; and, after six times, 52 per cent. Following the hot water treatment, the corresponding figures were 28 per cent, 21 per cent, and 5 per cent. It is evident that damaged seed coats are conducive to greater injury from the hot water treatment. In this experiment, the average reduction in emergence resulting from the hot water treatment of seed threshed once was greater than usual for two reasons: The seed was pre-soaked longer than usual before treatment and one of the samples was particularly sensitive to heat.

GREENHOUSE EXPERIMENTS ON THE CONTROL OF SMUT

Concurrent with the studies reported above, numerous small samples of naturally infected barley seed were treated and sown in glazed earthenware crocks in the greenhouse. The schedule of treatment varied somewhat according to the stage of development of these investigations at the time the different tests were made. Among the sixteen samples of barley tested in this way, at least five of the commonly grown varieties were represented. The average percentage of infected plants in the checks was 8.5. This percentage is not high, but it is representative of the higher infections found in the field in this region. The pre-soak period was usually four or five hours. The temperature of the water bath was 125° F. in most cases, but temperatures of 126°, 127° and 128° F. were used in some of the tests. In only one test out of sixteen did the treatment fail to give complete control of the disease. In this case, the temperature of the water bath was 125° F. As to the effect of the hot water treatment on the yields, the average number of healthy heads in the treated crocks was 54 per cent of the number in the untreated crocks.

One of the samples used in the above-mentioned tests had about 18 per cent of its seeds infected. Its seeds were plump, but they germinated rather poorly, even when untreated. The hulls had been broken off to a considerable extent in the threshing, and the sample suffered severely from the hot water treatment. Two more tests were conducted with it to study its reaction and that of the fungus to milder treatments. The results are summarized in Table 1.

In these tests the pre-soak period was 5 hours. Perfect control was secured by treating the seed for 11 minutes at 122° F. and 124° F. At 120° F., considerable disease developed, and, at 118° F., there was almost

TABLE 1.—EFFECTS OF APPLYING THE HOT WATER TREATMENT AT RELATIVELY LOW TEMPERATURES TO A SAMPLE OF SEED BARLEY

Treatment	Percentage emergence		Percentage diseased	
	First test	Second test	First test	Second test
Untreated check	86.6	89.3	20.6	17.0
Hot water (118° F.)	—	64.2	—	15.6
Hot water (120° F.)	58.3	60.6	3.0	6.2
Hot water (122° F.)	61.4	54.3	0.0	0.0
Hot water (124° F.)	40.0	—	0.0	—

as much smut as in the untreated check. This sample again proved to be very susceptible to heat injury. There was more damage to the seed from treating at 122° F. than ordinarily occurs from treating at 126° F.

After a study of the effect of the pre-soak period on germination had shown that shortening this period reduced the injury to the seed, a test was conducted in the greenhouse to find out how much it could be shortened without interfering with the control of the disease. Three samples of infected barley were used. These were treated for 11 minutes at 126° F., after different portions had been pre-soaked for periods of 2, 3, and 4 hours. About 120 seeds of each variety were subjected to each variation of the treatment. These were sown in a large flat on a greenhouse bench in rows six inches apart. The results of this test are shown in Table 2.

TABLE 2.—INFLUENCE OF THE PRE-SOAK PERIOD ON CONTROL OF SMUT

Sample	Percentage infection in check	Percentage infection after treatment		
		2-hour pre-soak	3-hour pre-soak	4-hour pre-soak
1	7	1.4	0.0	0.0
2	4	2.0	1.0	0.0
3	23	20.0	13.0	4.0

From these results it appears that a longer periof of pre-soak is required for some seed samples than for others. Possibly the condition of the seed coats and rapidity with which water enters the embryo may govern the time required for pre-soaking to ensure the destruction of the parasite within the seed by the hot water bath.

FIELD EXPERIMENTS ON THE CONTROL OF SMUT

A number of tests were conducted over a period of years under field conditions. In these tests, larger populations were used than in the greenhouse tests, but the hot water treatment was applied with the same apparatus as was used in the greenhouse tests. The number of heads in the check rows varied from 500 to 1,500, depending on the variety and the yearly rainfall and other environmental conditions. The pre-soak period was usually 4 or 5 hours. The duration of the hot water bath was 11 minutes. The temperature of the hot water bath varied in different tests

and, in some cases, several temperatures were tried with replicate lots of the same sample of seed. All of the seed used bore a natural infection of *U. nuda*. The results of these tests are summarized in Table 3. The percentages of smut are based on the total number of heads, healthy and smutted, but the reductions in yield are based on the number of healthy heads produced in check and treated rows.

TABLE 3.—FIELD TESTS OF THE HOT WATER TREATMENT FOR THE CONTROL OF SMUT

Sample	Percentage of smut and percentage reductions in number of healthy heads										
	Check smut	124° F.		125° F.		126° F.		127° F.		128° F.	
		Smut	Reduction	Smut	Reduction	Smut	Reduction	Smut	Reduction	Smut	Reduction
1	5	0	7	—	—	0	17	—	—	—	—
2	24	—	—	—	—	—	—	0	55	—	—
3	27	—	—	—	—	—	—	0	−23	—	—
4	18	—	—	—	—	—	—	0	73	—	—
5	14	—	—	—	—	—	—	0	33	—	—
6	24	—	—	0	53	—	—	0	69	—	—
7	17	—	—	0	30	—	—	0	53	—	—
8	12	0.1	1	—	—	0.8	14	—	—	0	50
9	11	0	28	—	—	0	47	—	—	0	54
10	11	0	16	—	—	0.05	28	—	—	—	—
11	4	0	22	—	—	0	32	—	—	0	80
12	4	0.2	13	—	—	0	11	—	—	0	54
13	8	0	15	—	—	0	30	—	—	0	63
14	6	0	−5	—	—	0	0	—	—	0	6
15	6	0.2	22	—	—	0	31	—	—	0	28
16	3	0	13	—	—	0	30	—	—	0	74
17	25	0	17	—	—	0	34	—	—	0	76

In the seventeen samples that were tested under field conditions, the average infection of the untreated check rows was 12.9 per cent. As a number of them were not treated at more than one or two temperatures, the average results of the whole series would not give good comparisons. However, nine of the samples were treated at three different temperatures, and direct comparisons can be made with these. At 124° F., the average infection in these nine samples was 0.06 per cent and the average reduction in the number of healthy heads was 14 per cent. At a temperature of 126° F., these two items were 0.09 and 25 per cent, respectively. When the temperature of the water bath was held at 128° F., there was no infection whatsoever but the yield was reduced by 54 per cent.

As a certain amount of infection seemed likely to survive the hot water treatment if the pre-soak period was too short, a field test was conducted on the following plan. Five samples of naturally infected barley were used and portions of each were treated at two different temperatures, namely 126° F. and 127° F., for a period of 11 minutes. Three different periods of pre-soak at a temperature of 70° F. were tried with each. The portions to be treated at 126° F. were pre-soaked for periods of 4, 5, and 6 hours. Those to be treated at 127° F. were pre-soaked for 3, 4, and 5 hours. There were five replications of every treatment in each sample and ten replications of the check. A summary of the results is shown in Table 4.

TABLE 4.—RESULTS OF FIELD EXPERIMENTS TO CONTROL THE LOOSE SMUT OF BARLEY BY MEANS OF THE HOT WATER TREATMENT, APPLIED AT TWO TEMPERATURES AND WITH VARIATIONS IN THE PRE-SOAK PERIOD

Treatment		Number of heads		Percentage infection	Percentage reduction in yield
Pre-soak period	Temperature of water bath	Healthy	Diseased		
Check	—	9344	665	7.1	Nil
4 hours	126° F.	3277	0	0.0	30
5 hours	126° F.	2671	0	0.0	43
6 hours	126° F.	2121	0	0.0	55
3 hours	127° F.	3358	2	0.06	28
4 hours	127° F.	2530	1	0.04	41
5 hours	127° F.	2083	0	0.0	51

The results summarized in Table 4 show that four out of six of the variations of the hot water treatment employed in this test gave perfect control of the smut. However, a small amount of smut appeared after pre-soaking for 3 hours and 4 hours and treating at 127° F. The results of this experiment show that pre-soaking the seed for 5 hours at 70° F. and treating it for 11 minutes at either 126° F. or 127° F. will give perfect control of the disease, but that treating at the higher temperature will result in poorer germination and yield. The reductions in the number of healthy heads show clearly that increasing the length of the pre-soak period or raising the temperature of the main water bath tends to injure the seed and to decrease the yield.

HOT WATER TREATMENT ON A LARGER SCALE

By means of the specially designed baskets, mentioned under "Materials and Methods", several lots of barley seed consisting of from 2 to 5 bushels each were treated at different times over a period of years with quite satisfactory results (15). In 1949, however, five lots of Montcalm barley were treated, and in only one lot was perfect control secured. In all of these larger scale treatments, the seed was pre-soaked at a temperature of about 70° F. and immersed in hot water at 126° F. for 11 minutes. Formerly the seed was pre-soaked for a period of 5 hours, but in 1949 the period was shortened to 4 hours to reduce the amount of injury to the seed. Apparently 4 hours' pre-soak at a temperature of 70° F. was too short, for in four out of five of these samples the average reduction in emergence, resulting from the hot water treatment, was negligible and the control of the smut was not satisfactory.

DISCUSSION

It is obvious, from the results of previous workers and from the experimental data presented in this paper, that satisfactory results from the hot water treatment can be achieved if a proper schedule for its application is followed. However, to secure good control of loose smut without undue injury to the seed, each step in the process must receive proper attention.

Pre-soaking the seed is a very important part of the hot water treatment. The results obtained by Appel (5), Dieudonne and Vanderwalle (6), and Gassner and Kirchhoff (10) stress this point. In one of the tests

described in this paper, the author found that the hot water treatment had very little effect on the viability of the seed when pre-soaking was omitted. The data in Table 2 show that pre-soaking the seed makes a great difference to the efficiency of the hot water bath in destroying the fungus.

It is necessary to regulate the temperature at which the seed is pre-soaked as well as to determine the amount of time to be allotted to this operation. According to Güssow and Conners (11), Appel secured complete control by pre-soaking the seed at 86° F. for four hours and incomplete control by pre-soaking it at 64° F. for the same period, followed in each case by the same treatment in the hot water bath. Winkelman (18) specified that the pre-soak should be carried out at a temperature between 76° F. and 87° F. Gassner and Kirchhoff (10) emphasized the marked effect which temperature exerts upon the rapidity with which water is taken in by the seed, the rate of absorption in their tests being 4 times as great at a temperature of 86° F. as it was at 50° F.

The length of time that the seed should be pre-soaked to give best results depends upon several factors, such as the temperature of the water in which the seed is pre-soaked, the condition of the seed coats, and the temperature and the duration of the hot water bath. Gassner and Kirchhoff (10) considered that from 60 to 70 parts of water should be taken up by the embryo to ensure complete control of the disease by a bath of 10 minutes at 125.6° F. Vanderwalle and Larose (17) reported equally good results from pre-soaking for 3.5 hours at 86° F. followed by 10 minutes at 122° F., and as from pre-soaking for 5 hours at 86° F. followed by 15 minutes at 118.4°F. As shown in Table 2, the author found that a 2-hour pre-soak at 70° F. was quite inadequate when followed by a treatment for 11 minutes at 126° F.; a 3-hour pre-soak was somewhat better, but even a 4-hour pre-soak was not sufficient in one case. But in the field test, summarized in Table 4, perfect control was secured by pre-soaking the seed for 5 hours at 70° F. The influence of the length of the pre-soak period upon the viability of the treated seed is strikingly shown in Figure 1.

The temperature of the hot water bath should be chosen to fit in with the pre-soak used and with the length of time the seed is held in the bath. Figure 2 shows the effect of different temperatures on the germination of the seed, and Tables 1 and 3 show the influence of various temperatures on both the seed and the disease. As would be expected, increases in the temperature of the water bath result in increases in seed injury, but the temperature must be sufficiently high to cause some injury to germination or else satisfactory control is not secured. In the present investigations, the reduction in germination usually ranged from 10 to 30 per cent when the disease was completely eliminated. When the seed coats were badly broken by the threshing operation, reduction in germination was sometimes higher. In Saskatchewan, barley is frequently very dry and brittle when threshed and considerable seed-coat breakage results. The treatment of very badly damaged seed with hot water should be avoided.

Different workers have favoured different periods of time for the immersion of the seed in the hot water bath. The standard period recommended in this country has been 10 minutes after a preliminary dip of two

minutes in water slightly cooler than the bath. The author believes that a preliminary dip is unnecessary if facilities are present for supplying a relatively large amount of hot water in relation to the quantity of seed placed in the bath and if facilities are available for quickly restoring the proper temperature of the water when the seed is first placed in it. Hence a period of 11 minutes was adopted to make up for the omission of the preliminary dip.

Previous work by various investigators has shown that different samples of grain vary greatly in their susceptibility to injury from the hot water treatment. The results of the present investigations bear out this fact. For instance, the data presented in Table 3 show that, when the seed was treated at 126° F., the reductions in yield varied from nil to 47 per cent. It is felt that one of the main reasons for this phenomenon is differences in the soundness of the seed coats. Tapke (16) showed that the hot water treatment caused more injury to seed wheat when the grain had been threshed by machine than when it had been threshed by hand. The germination tests with seed run through a small thresher, referred to earlier in this paper, showed that the percentage germination of barley seed fell off with increased damage to the hulls and seed coats caused by repeated threshings. On the other hand, it is possible that different varieties of barley differ in their ability to withstand high temperatures in the water bath.

From the results of tests described in this paper, it appears that treated seed, after it is dried, can be stored for a considerable length of time without much reduction in germination when it is sown. The maximum time between treating and sowing in these tests was 35 days, but it is probable that treated seed, if properly dried and stored, could be kept for much longer periods without any marked loss in viability.

There are two hypotheses which may account for the control of *U. nuda* by means of the hot water treatment. The first assumes that the fungus is killed and that the infected embryo of the seed survives the treatment. The second assumes that the embryos carrying the smut are weak and all of them are killed by the treatment, that is to say, if no smut survives. In Table 1 it is shown that treatment at 118° F. reduced germination from 89.3 to 64.2 per cent, a drop of 25.1 or approximately 30 per cent of the emergence of the untreated check. At the same time, the percentage infection was reduced from 17 to 15.6, a drop of 1.4 or about 8 per cent of the infection in the untreated check. This suggests that the infected embryos were not particularly weak, for, of the 25 embryos killed, only 2 were infected.

The following schedule for the application of the hot water treatment to barley seed has given good results during these investigations. Pre-soak the seed in water for five hours at a temperature of about 70° F.; dip the seed for 11 minutes in hot water held at 126° F.; cool immediately in cold water at the end of the 11-minute period; then spread the seed out to dry, and sow it after it has been dried well. It is by no means suggested that this is the only schedule which will give satisfactory results. For example, the seed may be pre-soaked for less time, provided that it is soaked at a higher temperature, as suggested by Lansade (14); or the time and tem-

perature of the hot water bath may be changed. The main point to keep in mind is that the schedule selected should eliminate the smut without causing more damage to the seed than is really necessary.

From the practical standpoint, the use of wire screen baskets is preferable to the use of bags for dipping the seed in the hot water bath. Hanna and Popp (12) did not secure satisfactory results when they treated half-bushel lots in bags, because of the difficulty in heating the seed uniformly.

Several types of machines, such as the Wisconsin hot water treater (4), are now in use in the United States and Canada. By means of these, infected seed can be treated on a comparatively large scale, and they should prove a valuable aid in reducing the amount of loose smut in these two countries.

SUMMARY

1. It is shown that the hot water treatment, applied according to a suitable schedule, will give satisfactory control of the loose smut of barley. However, the treatment generally interferes more or less with the germination of the seed.

2. Raising the temperature or lengthening the time of the pre-soak tends to increase the injury to the seed. Up to a point, each also tends to increase the efficiency of the treatment.

3. Similarly, raising the temperature of the water bath or lengthening the time of treatment causes greater injury to the seed and more thorough destruction of the parasite.

4. The following schedule has been found to give satisfactory results: Pre-soak the seed for five hours at a temperature of 70° F., dip it for 11 minutes in water held at 126° F., cool it immediately with cold water, and dry it well. Other schedules in which the separate steps are properly balanced should give equally good results.

5. It is important that the seed should all become heated to the same degree and at the same rate when it is placed in the hot water bath. For this purpose wire screen baskets are more satisfactory than bags.

6. It is desirable that threshing should be done in such a way as to minimize mechanical injury to barley if the seed is to be treated with hot water.

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VARIATIONS IN VITAMIN CONTENT WITH METHOD OF CURE AND STAGE OF GROWTH OF ALFALFA AND OATS AND THEIR UTILIZATION AS FORAGES BY LAMBS[1]

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The effects of method of cure and stage of growth of plants used as feed for live stock has been the subject of much research. It is now generally accepted that artificial curing of hay is the most efficient method of preservation of vitamins (4, 6, 7, 16) while sun-curing is the most destructive. For most vitamins there is a decrease in their content as the plants mature (3, 9, 17, 19, 24). This indicates the importance of considering these factors when preparing plants as feed for live stock.

Cured forages constitute the major means of satisfying the vitamin A requirements of live stock not on pasture and they also contribute significant amounts of thiamine and riboflavin when incorporated in the rations of non-herbivors. Hence, in view of the established effects of plant maturity and of curing method upon roughage quality, and in view of the supplementary relationships between forages and concentrates in feeding practices, it was deemed worth-while to extend the vitamin assays (23) to include a study of certain forages.

Alfalfa and oats were collected at different stages of growth, cured by several methods, and finally subjected to analysis for thiamine, riboflavin and carotene. The final phase of the study was a feeding experiment in which growth and vitamin A status of blood and liver in feeder lambs were examined.

EXPERIMENTAL PROCEDURE

During the course of this investigation, two series of experiments were undertaken. In 1946, samples of alfalfa and oats were taken at various stages of maturity, cured by different methods, and analysed for thiamine, riboflavin, and carotene. This work was extended in 1948 to include animal feeding trials in a study of carotene content of similar forages and its effect on the vitamin A status of the animals.

First Experiment

The experiment was designed to determine the effects of a number of factors on the vitamin contents of forage crops. Alfalfa (Grimm) and oats (Ajax) were grown on the University Seed Farm in six-row plots replicated in two blocks according to dates of seeding. The plots were harvested at weekly intervals, the first date in each case being the stage just before flowering. Each cutting was divided into three parts of approximately one pound each. The first portion was dried in an oven (11) over-

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night at 62° C., the second portion in a loft at 18°-23° C. and the third left in the field and turned periodically to expose all parts to the sun. The cured material was ground in a Wiley Mill (sieve openings 1 mm.) and stored in cartons in cold storage at −20° C. Analyses were made for thiamine, riboflavin, and carotene.

Second Experiment

Forages

This experiment was set up to study carotene values in alfalfa and oats as affecting the vitamin A status of feeder lambs. An attempt was made to repeat the first experiment on a larger scale to include feeding trials. The same varieties of forage were used, and were cut at two stages of growth corresponding to the first and last stages in the first experiment. The methods of cure were also similar. The dried forages were then chopped in a cutting box, thoroughly mixed, bagged and stored in a loft.

Animals

Forty-eight range wether lambs, averaging 65 pounds in weight and 165 days of age, were employed in this experiment. These were divided into twelve groups consisting of two Rambouillets, one Targhee, and one Romnellet per group. The animals were fed low carotene hay until placed in the pens, when they were started on assigned forage rations. The forage was supplemented with a concentrate, adjusted so that each animal received about 12 per cent crude protein. The concentrate for alfalfa forage was made up of beet pulp and oat grain, while that for oat forage contained beet pulp, linseed meal, and oat grain, with ground limestone and iodized salt added in each case. Feedingstuffs analyses of forage and concentrate fed to the lambs were made and total digestible nutrients calculated with assumed digestion coefficients (15).

The lambs were fed individually twice daily and had access to fresh water. Outdoor exercise was allowed for 5 to 6 hours daily, and the animals were bedded with shavings.

Criteria

Data on weights included initial, bi-weekly, and final weights, as well as hot and cold carcass weights. Blood samples, obtained for carotene and vitamin A analyses, were taken at the beginning of the experiment and at the time of slaughtering, and were prepared for analysis according to Kimble (10). Five ml. of plasma from each sample were kept frozen until required for analysis. Bessey *et al.* (2) found no detectable change in vitamin A and carotene content in blood after one month's storage at either 4° C. or − 20° C. Liver samples for vitamin A and carotene determinations, were stored at − 23° C. after quick freezing.

Chemical Analyses

The moisture content of forage was determined by oven-drying at 130° C. for one hour. The crude protein, crude fat, crude fibre, ash, and N.F.E. were determined by the usual feedingstuffs methods. Thiamine was determined by the method of Hennessy (8), modified by Spencer *et al.* (22). It was found necessary for optimal oxidation of thiamine in forage

crops to use 5 per cent potassium ferricyanide instead of 1 per cent as used for cereal grains. Riboflavin was determined by the method of Andrews (1), as modified by Spencer *et al.* (22). The method of Nelson (12) was used for determination of carotene, precautions being taken to saturate the column with carotene prior to its assay. For the determination of vitamin A in blood plasma, the method of Kimble (10) was adapted for use with glycerol dichlorohydrin (20, 21). The liver samples were thawed at room temperature, minced, and vitamin A determined according to the method of Gallup and Hoefer (5).

EXPERIMENTAL RESULTS AND DISCUSSION

First Experiment

The values for thiamine, riboflavin and carotene in alfalfa and oats, as affected by stage of growth and method of cure, are summarized in Table 1. Each value represents a mean of duplicate analyses in each replicate, expressed in μgm. per gm. of dry matter.

Considering the effects of methods of curing, these data reveal that the greatest vitamin retention was obtained by oven-drying, and the least by sun-curing. Of the three vitamins studied, carotene was most seriously affected, with a decrease from 482 to 131 μgm./gm.

TABLE 1.—MEAN THIAMINE, RIBOFLAVIN, AND CAROTENE VALUES GROUPED ACCORDING TO DATES OF CUTTING AND METHODS OF CURE

(μgm./gm. Dry Basis)

Method of cure	Thiamine			Riboflavin			Carotene		
Date of cutting	Oven	Sun	Dark	Oven	Sun	Dark	Oven	Sun	Dark
				Alfalfa					
June 4	5.59	4.49	4.44	11.97	9.14	11.38	577	168	447
June 11	4.97	3.74	3.65	11.29	10.56	10.94	564	135	458
June 17	4.08	2.92	3.04	10.21	10.07	9.52	505	140	492
June 22	4.56	3.90	3.46	9.60	9.18	9.62	465	120	410
July 2	3.85	2.98	2.95	9.03	8.60	8.65	401	114	375
July 9	4.75	2.58	2.52	8.77	8.06	6.33	383	111	381
Mean	4.63	3.35	3.26	10.14	9.27	9.74	482	131	427
				Oats					
June 24	3.28	4.60	3.52	7.79	7.12	7.88	331	186	294
July 2	3.40	2.75	3.58	7.02	6.49	6.85	260	93	200
July 12	2.92	2.74	3.28	6.70	5.31	5.91	271	47	199
July 20	3.44	3.61	3.26	5.87	5.53	5.62	234	100	155
July 26	3.98	2.77	3.69	4.77	3.17	3.56	159	80	151
Aug. 2	3.98	3.14	2.96	2.61	3.26	3.20	100	102	114
Mean	3.50	3.27	3.38	5.79	5.15	5.50	226	101	177

TABLE 2.—TOTAL DIGESTIBLE NUTRIENT CONSUMPTION, GAINS AND FEED EFFICIENCY

Forage	Stage	Cure	T.D.N. (average lb.)	Gain (average lb.)	Feed efficiency*
Alfalfa	First	Drier	98.4	19.6	4.89
		Sun	80.3	15.3	5.29
		Loft	87.4	17.0	5.32
	Second	Drier	86.4	19.7	4.44
		Sun	87.7	15.2	5.84
		Loft	92.7	14.0	6.87
Oats	First	Drier	91.9	15.4	6.11
		Sun	90.6	14.0	6.56
		Loft	88.7	11.7	8.70
	Second	Drier	92.2	14.2	6.72
		Sun	87.3	9.7	10.49
		Loft	92.1	12.8	7.47
		Mean	88.4	14.9	6.56

* Feed efficiency value is based on T.D.N. consumed per pound of gain made.

With regard to stages of growth, as shown by dates of cutting, the most significant changes occurred in riboflavin and carotene values. There was a consistent decrease in the values for these two vitamins with advancing maturity.

The trend of thiamine content in relation to maturity of the plant differed in oat and alfalfa forage. Whereas the values in alfalfa gradually declined, there was evidence, in the case of oats, that the corresponding decline of thiamine content in leaves and stems was overshadowed by an increase in the maturing kernel. These data support the findings that oats are higher in thiamine than other cereals, and Robinson *et al.* (14) who showed that as the oat plant ripens the thiamine concentrates in the kernel.

Generally speaking, the vitamin content decreased as alfalfa and oat plants matured. Artificial drying, without exception, resulted in greater vitamin retention, while the most serious losses, especially in carotene, were incurred by curing in the field.

TABLE 3.—GAINS OF LAMBS ADJUSTED FOR T.D.N. CONSUMPTION

Forage	T.D.N. (average lb.)	Gains (average lb.)	Adjusted gains (lb.)
Alfalfa	86.5	16.8	17.3*
Oats	90.5	13.0	12.5
First cutting	88.7	15.5	15.4
Second cutting	88.1	14.3	14.4
Drier-cured	91.0	17.2	16.6**
Sun-cured	86.5	13.6	14.0
Loft-cured	87.7	13.9	14.1
Mean	88.4	14.9	

* L.S.D. at 5 per cent level is 1.9.
** L.S.D. at 5 per cent level is 2.3.

TABLE 4.—DRESSING PERCENTAGE AND CARCASS GRADE

Forage	Stage	Cure	Dressing percentage	Carcass grade*
Alfalfa	First	Drier	46.8	87.8
		Sun	47.4	90.1
		Loft	46.8	91.3
	Second	Drier	48.3	89.0
		Sun	46.2	83.7
		Loft	46.5	82.3
Oats	First	Drier	45.4	80.3
		Sun	44.0	77.4
		Loft	43.9	83.0
	Second	Drier	45.2	80.8
		Sun	43.8	82.5
		Loft	44.6	80.1

* Carcass grade calculated on arbitrary basis of 32 per cent spread between top and bottom carcass.

Second Experiment

A summary of average total digestible nutrient consumption, gains and feed efficiency for each forage is given in Table 2. The feed efficiency values indicate that there was a difference between feeds, alfalfa being superior to oat hay. There was no indication of a difference due to methods of cure or stages of growth. After the gains were adjusted for T.D.N. consumption (18), it was revealed that they were significantly influenced by both the species of forage and the method of curing. Table 3 shows the summary of T.D.N. consumption, gains and adjusted mean gains.

It was found that the dressing percentage based on cold carcass weight was higher for lambs fed alfalfa than for those fed on oat forage. In carcass quality, the animals fed alfalfa were considered somewhat superior. There was no significant difference due to methods of cure or stages of growth. Data relative to carcasses are summarized in Table 4.

The results of the feeding experiment indicate that the carotene content of the forages influenced the vitamin status of the animals, in spite of the fact that the lambs were not initially depleted in vitamin A. No symptoms of vitamin A deficiency were observed during the study. In Table 5 is shown a summary of carotene consumption and vitamin A values in blood plasma and liver.

It was noted that even forages with comparatively low carotene content supplied considerably more than the 50-55 μgm. per kg. per day, suggested as necessary by Peirce (13) for animals recovering from night blindness. There was a gradual increase in vitamin A content in the blood during the experiment regardless of the kind of forage consumed. Only traces of carotene were found in blood plasma and liver.

Vitamin A storage in the liver was influenced by methods of curing as shown by the analysis of variance in Table 6, and which is further illustrated in Tables 7 and 8.

TABLE 5.—CAROTENE CONSUMPTION AND VITAMIN A CONTENT IN BLOOD PLASMA AND LIVER

Forage	Stage	Cure	Carotene consumed (average gm.)	Vitamin A Content		
				Blood	Plasma	Liver
				Initial (μgm./ml.)	Final (μgm./ml.)	(μgm./gm.)
Alfalfa	First	Drier	9.5	0.28	0.32	79.8
		Sun	7.1	0.32	0.64	71.8
		Loft	4.8	0.27	0.35	63.3
	Second	Drier	9.3	0.24	0.36	63.6
		Sun	1.3	0.20	0.27	32.2
		Loft	6.3	0.26	0.27	44.1
Oats	First	Drier	9.6	0.27	0.27	128.3
		Sun	1.9	0.23	0.29	37.4
		Loft	4.9	0.27	0.36	67.4
	Second	Drier	4.4	0.21	0.34	71.5
		Sun	2.3	0.27	0.33	44.5
		Loft	4.3	0.30	0.25	80.8

TABLE 6.—ANALYSIS OF VARIANCE—VITAMIN A CONTENT IN LIVER (μgm./gm.)

Variance due to	D.F.	Mean square
Feeds	1	1893.80
Growth	1	4138.51
Cure	2	6206.55*
F × G	1	497.29
F × C	2	1728.19
G × C	2	1146.29
F × G × C	2	2198.92
Error	36	1089.65
Total	47	

* Significant at 1 per cent level.

While liver-storage of vitamin A was influenced by the level of carotene consumption, the efficiency of conversion of carotene to vitamin A, or the ability of the body to retain it, appears to decrease as consumption of carotene is increased.

It is evident from this study that all forages tested supplied more than the minimum carotene requirements, as indicated by the general increase in vitamin A storage. No forage tested could be considered definitely inferior. Nevertheless, since those feeds high in carotene resulted in the most favourable response, it appears that high carotene content in forages is associated with higher nutritive value in general. It is worth-while to recall that, of the three vitamins studied, carotene was most readily affected by the treatment of the forage.

TABLE 7.—CAROTENE CONSUMPTION AND LIVER STORAGE OF VITAMIN A ARRANGED ACCORDING TO METHODS OF CURE OF FORAGE

Method of cure	Carotene consumption (average gm.)	Vitamin A in whole liver (average gm.)
Drier	8.2	42.8
Loft	5.0	30.3
Sun	3.2	22.4

TABLE 8.—CORRELATION BETWEEN CAROTENE CONSUMPTION AND LIVER STORAGE OF VITAMIN A

Source	D.F.	Correlation coefficient
Between crops, stages and interactions	3	
Between cures and interactions	8	0.8537*
Error	36	−0.0036

* Highly significant.

SUMMARY

Two investigations of the effects of stage of maturity and method of curing of alfalfa and oat forage are discussed.

In the first, thiamine, riboflavin and carotene content of the cured forages were determined and it was found that oven-drying (62° C.) effected the greatest vitamin preservation and field-curing the least, with loft-curing being intermediate. Values obtained at six stages of maturity indicated consistent decreases in vitamin contents with the exception of thiamine in oats. Carotene was most readily affected by curing and stage of maturity.

In the second, the forages were similarly cured but represented early and late stages only. The feeds thus obtained were individually fed over a 70-day period to fattening lambs receiving a concentrate allowance in addition. The gains of the lambs fed artificially-dried forages were greater than those receiving sun or loft-cured products. Forage treatments did not influence carcass quality although, as with gains, alfalfa-fed lambs were superior. Plasma vitamin A values did not reflect forage treatments but there was a significant positive correlation between carotene intake and liver vitamin A at slaughter.

While it is true that no forage tested was subjected to excessive weathering during curing, it is significant that those samples higher in carotene produced better responses in the feeding trial and, of the vitamins studied, carotene was most readily destroyed by adverse treatment of the forage.

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SOIL MICROFLORA IN RELATION TO MANGANESE DEFICIENCY[1]

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It has been demonstrated by Gerretsen (4, 5) and later, using Gerretsen's technique, by Leeper and Swaby (6) that manganese in the soil can be oxidized by the soil microflora. More recently, however, Bromfield and Skerman (2) reported that the organisms isolated on calcium citrate-manganous sulphate medium (5) were able to oxidize manganese only in the presence of citrate but not in the unsterilized soil-agar plaque. Therefore they concluded that the oxidation of manganese observed on a citrate medium is apparently due to a non-biological oxidation. The organisms, owing to their activity, increased the alkalinity of the medium and at this level of pH manganese is readily oxidized in the presence of oxyacids.

Continuing an investigation on the relationship of soil microflora to the manganese deficiency in soil (8, 9), several organisms capable of oxidizing manganous salts on artificial media as well as in soil agar plaques have been isolated on calcium citrate-manganous sulphate agar (5).

The organisms isolated from these soils belong to several groups of bacteria, proactinomycetes, actionomycetes and fungi. The following fungi proved to be able to oxidize manganese on calcium citrate-manganous sulphate medium as well as in the soil-agar plaques: *Helminthosporium victoriae*, *Culvularia lunata*, *C. brachyspora*, *C. inaequalis*, *Periconia circinata*, *Cephalosporium* sp. and several as yet unidentified cultures. These organisms also were able to oxidize manganese in media containing only manganous salts of manganese, agar and tap-water. The data presented in Table 1 indicate that these fungi were capable of oxidizing manganese in these simple media. However, a culture of bacterium was able to oxidize manganese only from the citrate salt. On inoculation of these fungi into soil-agar plaques (Gerretsen's modified technique) the organisms were capable of oxidizing $MnSO_4 . H_2O$ in sterilized as well as in unsterilized soil. From Figure 1, it is quite apparent that various nitrogenous compounds added to the soil prior to plating (to give equivalent weights of N) influenced the intensity of manganese oxidation. Thus, addition of asparagine stimulated the process of oxidation, whereas addition of $Ca(NO_3)_2$ retarded it. Apparently different sources of nitrogen affected the metabolic processes of the organisms differently.

In this respect Funchess (3) and later Ridalevskaya (7) demonstrated that soils with strong nitrifying power or on the application of nitrates tended to increase the water-soluble fraction of manganese in the treated soils. Furthermore, it has been shown by Bokuchava (1) that nitrates are able to inhibit the activity of catalase. Taking these findings into consideration, it is possible to assume that the application of different nitrogenous fertilizers may affect not only the rate of their growth (Figure 1) but also the activity of their metabolic by-products as well.

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[1] Contribution No. 304 (Journal Series) from Division of Bacteriology and Dairy Research, Science Service, Canada Department of Agriculture, Ottawa.

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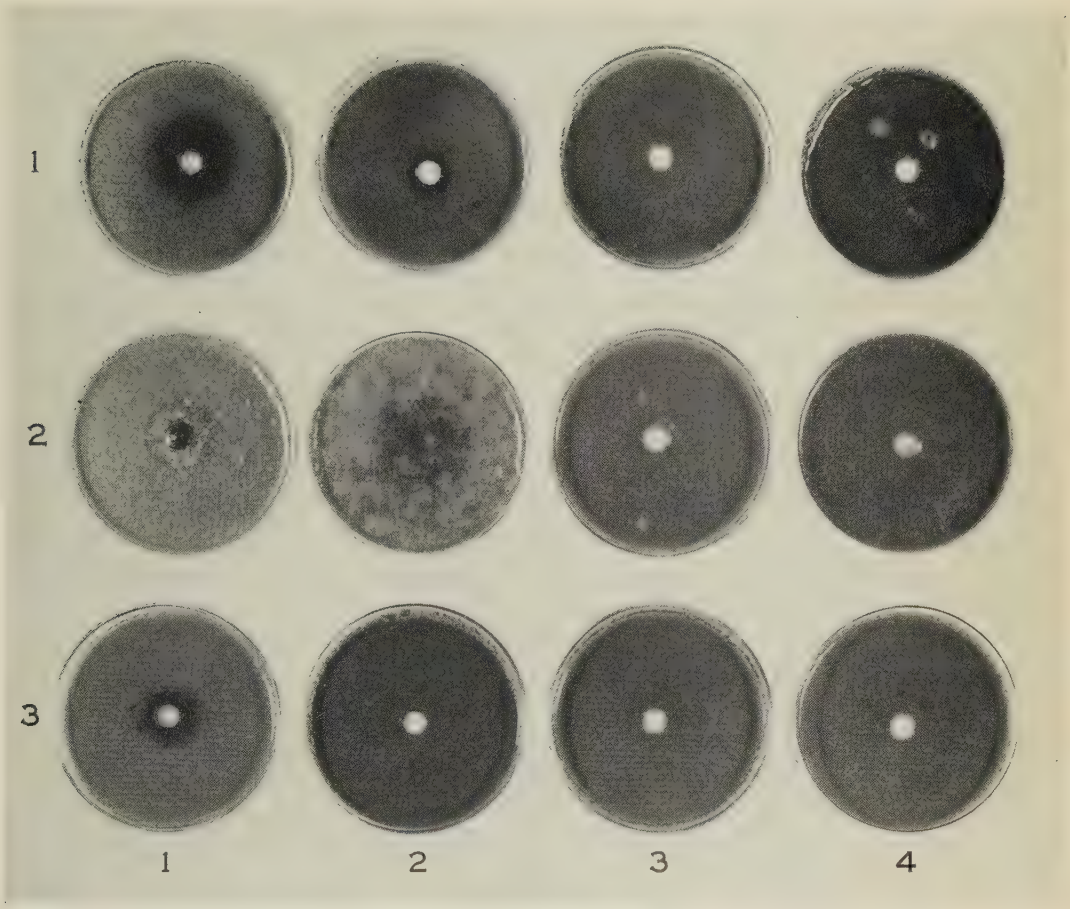

FIGURE 1. Influence of Different Sources of N on the Rate of Oxidation of $MnSO_4$ (incubation—6 days at 23° C.).

Horizontal rows 1—Control soil
2—Asparagine added,
3—$Ca(NO_3)_2$ added.

Vertical rows 1—Sterilized, inoculated,
2—Unsterilized, inoculated,
3—Sterilized, not inoculated,
4—Unsterilized, not inoculated.

The results herewith presented indicate that it is possible by means of Gerretsen's method to isolate fungi capable of oxidizing manganese without the presence of citrate in artificial media. Furthermore, when these organisms were introduced into a soil-agar plaque they were able to oxidize manganous sulphate in sterilized as well as in unsterilized soil.

TABLE 1.—OXIDATION OF DIFFERENT MANGANOUS SALTS BY SOIL MICRO-ORGANISMS

Organisms	$MnCO_3$	$MnCl_2$	$MnSO_4$	Mn. Citrate
C. brachyspora	+ + + +	+ +	+ + +	+ + + +
C. lunata S	+ +	+ + +	+ + + +	+ + + +
C. inaequalis	0	+ +	+ + +	+ + + +
P. circinata	0	+ + + +	±	+ + + +
N-4-2 (F)	+ + + +	+ + + −	+ + +	+ + + +
Bact. N-4-Mn	0	0	0	+ +

Rate of oxidation:
+ + + + Very good
+ + + Good,
+ + Fair,
+ Poor,
0 No oxidation.

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